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ON THE EQUILIBRIUM STATE OF THE INTERACTING POPULATION OF AN INSECT AND ITS PARASITE [1]

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INTRODUCTION

The fluctuation of the population density is a fundamental problem in animal ecology, and that of insect pests is also important from an economic viewpoint. Climate is said to play an important and decisive rôle as an environmental factor for the determination of population density, while it is claimed also that biotic factors regulate the fluctuation of the population density. The supposition that the population is maintained at a state of equilibrium where the density of the population fluctuates in a regular manner was proposed by Howard and his followers. This supposition was demonstrated theoretically by several mathematicians such as Lotka and Volterra.

Gause ('34, '36), working with unicellular organisms and granary mites, demonstrated the fluctuations of population densities in the interacting populations, and made many important findings. DeBach and Smith ('41), working with two interacting species of insects, the house fly *Musca domestica* and its parasite *Mormoniella vitripennis,* showed the soundness of the mathematical system of Nicholson and Bailey. The present author studied the interaction between the azuki bean weevil *Callosobruchus chinensis* and its larval parasite *Heterospilus prosopidis* and demonstrated the fluctuation of the population density of both species without ignoring the effect of the density of the host on its own reproduction (Utida, '49).

This investigation attempts to determine experimentally whether or not the interaction of a host and parasite, under constant environmental conditions, causes a fluctuation in their population densities. The present work is also concerned with the mechanism which determines the density of the host and parasite species when they are in a state of equilibrium.

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MATERIALS AND METHODS

The population studied was that of the azuki bean weevil, *Callosobruchus chinensis* L., and the pteromalid parasite, *Neocatolaccus mamezophagus* Ishii et Nagasawa. Both the host and parasite species have been reared in the laboratory, under controlled conditions for several years.

The universe for each host-parasite population was a petri dish, 1.8 cm. high and 8.5 cm. in diameter, held in an incubator at a constant temperature of 30° C. The relative humidity was maintained at 75 per cent, by using the method of Zwölfer ('32). Ten grams (about 50–

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60 seeds) of the azuki bean, variety Dainagon, with a water content of about 15.3 per cent, were placed in each petri dish at the beginning of the experiment. The food was replaced every three weeks, the time required for a generation of the host insect, by a fresh ten-gram lot.

At the beginning of the experiment, 8 pairs of weevils were collected, within one hour of emergence, from the stock culture and placed inside each petri dish. When 10 weeks had elapsed after the start of the experiment, 4 pairs of parasitic wasps were collected from the stock culture and were introduced into each breeding dish of the weevils. The number of each sex of dead adults and living adults of both species was recorded, from the beginning of the experiment, at weekly intervals. Living adults were lightly anesthetized (with ether), counted, then put back in the breeding dish. At each new supply of beans, the remnants of the food which had been in each breeding dish for the three previous weeks were placed in separate petri dishes. Population counts in these dishes were also made of the adults which emerged for 6 weeks after the separation.

Two experimental populations were run in the petri dishes. The counts, both of host weevils and of parasitic wasps, of the two populations were continued over a period of three years, covering 51 generations of the host.

Results

The number of living and dead individuals of both species was counted weekly as has been stated above. The number of adults emerging between two successive counts was not directly observed. It can be determined from the number of adults alive on two successive counts and the number of dead individuals counted on the second of the successive counts.

The results of the counts on both host and parasite populations show that the number of living individuals, the number of dead individuals, and the number of emerged individuals increase and decrease, in turn, within a period of three weeks. In the case of the bean weevil, this fluctuation of population density is apparently caused by the emergence and death of adults belonging to each generation. It can not be considered a result of host-parasite interaction. In the case of the parasites, the population density also moves up and down in each generation and the fluctuations closely coincide with those of the weevil population. This may be caused by the fact that the life cycle of the wasp synchronizes successfully with that of the weevil, although the mean duration of a life cycle of the parasite is about two weeks while that of the host is about three weeks.

The fluctuation of an insect population can be classified into three categories according to its cause; (1) the increase and decrease caused by the emergence and death of the individuals belonging to the same generation, (2) fluctuations associated with changes in climate, and (3) fluctuations caused by environmental factors of a biotic nature, such as a host-parasite interaction. Under the experimental conditions, climate is constant and so item (2) is eliminated. The fluctuation within a period of about 3 weeks observed in the results of the present work corresponds to item (1). To eliminate this fluctuation, the number of *emerging* individuals belonging to three successive counts can be summed. In such a way, the total number of hosts and parasites emerging in each generation can be obtained and these values are treated as the population densities in each generation. Since the fluctuation attributable to items (1) and (2) has been eliminated, there remains only the fluctuation belonging to item (3).

According to Nicholson ('33), the density of the host population exposed to the attack of the parasite is called the initial density of the host. The density of the hosts that escape the attack of the parasite and reach the adult stage is called the final density of the host. The initial

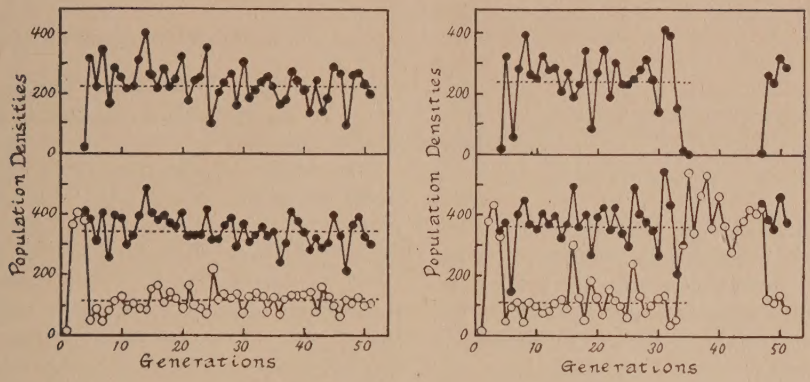

FIG. 1. Fluctuation of the population density: Population A (left) and B (right). Upper: parasite population. Lower: Initial host density (●) and final host density (○). Dotted line is the mean value.

density of the host in any generation can be obtained by adding the final density of the host to the density of the parasite in that generation. The assumption is made that a single host is consumed by an individual parasite and that there is no appreciable mortality of the host after it has passed the stage susceptible to parasitization.

In figure 1, the initial density and the final density of the host population and the density of the parasite population are shown for population A and for population B. In the beginning of each experiment, the host density increased rapidly. In the 2nd and 3rd generations the density was about 400 adults per petri dish and at this value the population saturated the given environment. After the introduction of 4 pairs of parasites to the petri dishes in the 4th generation, the final density of the host began to decrease. By the 5th generation, the host density reached a new and lower equilibrium. After this generation, the density fluctuated around a mean value. Both the initial density of the host and the density of the parasite fluctuated in a similar manner.

In population B, however, the final density of the host increased in the 34th generation and that of the parasite decreased. In the 35th generation, the parasite population was completely eliminated. In the 47th generation of the host, 4 pairs of the wasp were introduced from the routine culture of the stock and then the host density decreased.

The discussion below is restricted to those fluctuations of density observed from the 4th generation to the end of the experiment in population A and those from the 4th to the 34th generation in population B.

STATISTICAL EXAMINATION. I

The population densities fluctuate widely in rare cases, but they usually oscillate around a mean value. The question arises whether the fluctuations in the initial density of the host, in the final density of the host, and in the density of the parasite are caused by a host-parasite interaction or are the result of chance.

The total number of individuals counted in this experiment is very great, ranging from 4,000 to 10,000 in the three types of densities. The number of generations is 48 in population A and 31 in population B. The chance that a weevil or wasp may emerge in a particular generation is very small, being as low as $1/48$ or $1/31$. For these reasons, the frequency distribution of the population density in each generation would conform with the Poisson distribution, if the fluctuation was

TABLE I. *Lexis's ratio*

	Population A	Population B
Initial density of the hosts	7.8	15.4
Final density of the hosts	8.7	17.0
Density of the parasites	21.6	40.3

due to mere chance. Lexis's ratio (σ^2/m) is a good index for the conformity of the Poisson distribution with the given one. When this ratio is larger than unity, the given distribution is flatter than Poisson's theoretical one, and vice versa.

The results of the calculation are given in table I. The values of Lexis's ratio are far greater than unity in all cases. The frequency distribution of the population density in each generation is far flatter than the distribution provided by chance, or is hypernormal. This value is greater in the parasite population than in the host population and is only slightly greater in the final density of hosts than in the initial density of hosts.

It is concluded that the population densities of both host and parasite fluctuate far more widely than could be expected by mere chance and that the fluctuation is due to certain biological factors.

STATISTICAL EXAMINATION. II

The velocity curve of the original fluctuation is obtained simply by plotting the difference of density between two consecutive generations. A comparison between the curve of the original fluctuation and its velocity curve is made. It is found that a close correlation, negative in sign, exists between these two curves. But, even in a series of numbers taken at random, we can also find a close negative correlation. The value representing the probable aftereffect $\frac{\overline{\Delta^2}}{n^2 - \bar{n}^2}$ is a good index of this relation, where Δ^n is the difference of density between two consecutive generations and n is the density of a certain given generation. When the value $\frac{\overline{\Delta^2}}{n^2 - \bar{n}^2}$ is 2, the series of numbers is in random order. When this value is > 2 or < 2, the probable aftereffect is *reactive* or *inertiatic*.

The results of the calculation of this value are given in table II. All of the obtained values are > 2. It is concluded from this result that the probable after effect is *reactive* in its nature and the fluctuations of density are not in random order. The density of each generation is not independent and affects the density of the following generation in a *reactive* manner. When the density of a certain generation is high, the density of the next generation becomes low, and vice versa. In this way, the density always tends to approach the mean level of density.

TABLE II. *Calculated values of probability after effect,* $\frac{\overline{\Delta^2}}{n^2 - \bar{n}^2}$

	Population A	Population B
Initial density of the hosts	1.86	2.25
Final density of the hosts	1.72	1.99
Density of the parasites	2.13	1.95

CORRELATION COEFFICIENT

Next a question arises: what is the biological reason for the fluctuation of density? On the supposition proposed by Volterra, the fluctuations of the host and parasite densities would have a close correlation between them and a definite periodicity. A glance at the observed result does not show a regular fluctuation over a definite period. Therefore, it is very clear that the fluctuations obtained do not follow a simple mathematical concept.

The values of the correlation coefficient between the initial host density, the final host density, and the parasite density are given in table III.

The high correlation between the initial host density and the parasite density may be due to the fact that the emerging

TABLE III. *Correlation coefficients*

	Population A (values of r)	Population B (values of r)
Initial host density—Parasite density	0.885 ± 0.022	0.740 ± 0.056
Parasite density—Parasite density in the previous generation	-0.389 ± 0.084	-0.436 ± 0.099
Parasite density—Final host density	-0.576 ± 0.065	-0.590 ± 0.079
Initial host density—Final host density in the previous generation	0.317 ± 0.087	0.398 ± 0.105
Final host density—Reproductive rate of the host	-0.806 ± 0.034	-0.784 ± 0.047

number of parasites depends on the initial density of the hosts. The emerging number of parasites is partly dependent upon the number of parasites in the preceding generation. This is conceivable from the value of the correlation coefficient between them. This result accords with the result of a calculation as to the probable aftereffect between them. But, this effect is not so evident in contrast to the influence of the initial density of hosts upon the parasite population.

There is a negative correlation between the parasite density and the final density of the host. A close correlation is expected between the final density of the host and the initial density of the host in the same generation, since the change of the final density of the host depends upon the density of the parasite, which depends upon the initial density of the host. But the result of the calculation is contrary to this expectation.

A slightly positive correlation exists between the final host density and the initial host density in the next generation. When the weevil is reared independently of the parasite, the relationship between the final density of the host and the rate of reproduction of the host is represented by a curve which closely resembles a rectangular hyperbola. Since such a close relationship exists between these two factors, there exists, in a mixed population of the weevil and its parasite, a powerful regulation of the initial host density by the final host density of the previous generation. A high negative correlation exists between the final host density and the rate of reproduction of the host.

From the results mentioned above, it is concluded that the initial density of the host in a given generation is determined by the final density of the host in the previous generation, and that the initial density of the host determines the density of the parasite. The density of the parasite determines the final density of the host. It is clear, therefore, that the effect of host density on reproduction is operative in determining the initial density of the host and the density of the parasite.

PERIOD ANALYSIS OF THE FLUCTUATION

To find a period in the fluctuation obtained, Schuster's method of harmonic analysis cannot be applied, for the observed fluctuation has an aftereffect as mentioned above. When external forces act in an irregular manner on the given fluctuating system, where the amplitude, the phase, and the period may change, we can easily detect the period and the damping rate of the original system from the observed fluctuating system where the amplitude and the phase change, using the self-correlation method of period analysis which was discovered by Takahashi ('35). In the present experiment, the individual variation inherent in an animal population may disturb the original oscillation. Such ecological characters as reproductive potential, longevity, rate of reproduction, etc., have definite values, on an average, but show great differences when individual insects are examined. Therefore, this self-correlation method of period analysis is suitable for the present case.

The results of the analysis are given in figure 2. In each series, the curve in this figure is not periodic and represents a damped oscillation. Thus, the observed fluctuation does not belong to the true periodic fluctuation, but belongs to the so-called cyclic fluctuation, as designated by Fujiwhara and others ('37) for phenomena that fluctuate with variable periods but have a certain definite mean value. The maximum points in the curves (for example, 2, 4, 6, 8 and 12 generations on the final density of hosts in the population A and 3, 7, 10, 12 and 15 generations on that in population B) are to be considered as possible periods. Many of the maximum points obtained are within the range of probable error and cannot be significant as periods. The reliable values as periods are tabulated in table IV. The periods obtained are 3, 4, 5 or multiples of these.

It has been found by a Japanese physicist, Terada, that such a period of 3 is frequently observed even in a fluctuation of serial numbers in random order and this has been termed by him the apparent period or the quasi-period (Fujiwhara and others, '37). The following examination was made as to whether or not the period obtained belongs to this quasi-period. When a fluctuation is an apparent one, the frequency of generations, from a maximum to another maximum in the fluctuation, accords closely with the following formula, presented by Kameda,

$$N = \frac{2k(k-1)(k+2)}{(K+3)}\,Nt,$$

where K is the interval from a maximum to the next maximum in the series, N is the frequency of K, and Nt is the sum of the intervals. From a comparison of the

TABLE IV. *Obtained periods*

	Population A	Population B
Initial density of the host	5, 10, 15.	5, 11, 16.
Final density of the host	6.	3.
Density of the parasite	4, 7, 11, 15.	3.

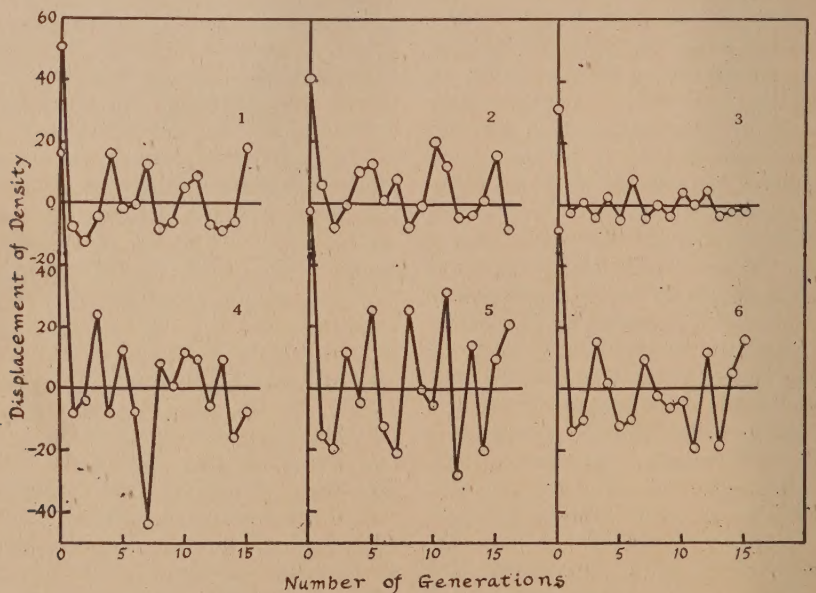

FIG. 2. Periodogram of the fluctuation. 1: Population A, density of the parasite. 2: Population A, initial density of the host. 3: Population A, final density of the host. 4: Population B, density of the parasite. 5: Population B, initial density of the host. 6: Population B, final density of the host.

observed frequency with the theoretical values (table IV), we can easily find the differences between them in each case. It is concluded, therefore, that the obtained values for a period do not always depend on the quasi-periodicity.

It is concluded that the fluctuations of the density in both populations are not apparent ones and cyclic in nature, but have a certain definite periodic value. The result obtained is contradictory to the theoretical expectation, made by several mathematicians such as Volterra and Lotka, that the lengths of period in host and parasite populations are not equal to each other. The factors operative in the present case may be beyond these simple mathematical concepts.

In protozoan populations, such a classical fluctuation as that expected by the mathematicians is not observed and a so-called relaxation oscillation is observed; that is, the prey is devoured completely by the predator which perishes before long for lack of food (Gause, '34). In an insect population, especially in the case of an interacting host and parasite, however, the relaxation oscillation may be observed, since the parasite can hardly parasitise the host completely whenever the parasite is very numerous. When the initial density of the host is greatly reduced by high parasitism, the parasites cannot find any host individuals and the parasite population perishes. Such a case does not occur once in 10 times in the cycles observed in population A and occurs only once in 6 times in the cycles of population B. Thus, the chance of this type of fluctuation may probably be below $\frac{1}{16}$. This type of fluctuation has been found in protozoan populations, when there is a refuge for the prey in the given environment (Gause, '34). In an insect population, where an interacting host and its parasite are observed, however, this type of fluctuation may occur even if the refuge does not exist in the given environment, since the efficiency of the parasite in finding a host depends on the density of the hosts.

Level of the Equilibrium State

The population density of an insect maintains a certain constant level at an equilibrium state where its biotic potential is balanced against environmental resistance. This fact has been shown in the single species populations of the flour beetle, the fruit fly, and the bean weevil (Utida, '41). In mixed populations of a host and its parasite, however, there is little experimental knowledge of the equilibrium state. Gause ('34, '36) worked with protozoa and mites, but his interest was mainly confined to the fluctuation of density and was not concerned with the equilibrium state itself.

Nicholson ('33) has said that the densities of the host and parasite populations continue to oscillate perpetually around the mean density. In other words, when the population density departs from the mean density in any definite generation, the density in the next generation comes back to the mean density, or the steady density, by an interaction between the two competing species. Against this idea of Nicholson, Uvarov ('31) has expressed his opinion in his work "Insects and Climate." When we suppose a condition in which the fluctuation of population density is observed in a census covering several generations, the density of each census will fluctuate around the mean value of the total counts of census. Can we conceive this mean value as a steady density at an equilibrium state? Is this a proof for the existence of a steady density? The only evidence on which to make such a claim would be the fact that there is a mean value in a certain definite series of numbers and that is a foolish idea. This concept is a protest against the idea that an equilibrium state really exists in a population.

It is clear, as mentioned above, that the probable aftereffect is *reactive,* and the density in each generation will constantly approach the mean value. The mean density obtained in this experiment is not a mere mean value, and corresponds to

the steady density in Nicholson's sense. An equilibrium state exists clearly in the population and it is not a fantastic idea.

What mechanism operates in the determination of the steady density of populations which are in a state of equilibrium? According to Nicholson's theory, the level of the steady density of both host and parasite populations can be calculated from the numerical values of the rate of reproduction of the host species and of the parasite host-finding ability, under the assumption that a parasite searches for hosts at random in a given environment. In Nicholson's theory, a definite constant value is given to the reproductive rate of the host on the assumption that the effect of host density to the rate of its own reproduction is not operative.

In the writer's opinion, however, in a mixed population of the host and its parasite the effect of host density may not be overlooked, just as it may not be overlooked in a single-species population where the steady density of the host population is determined by the effect of density on its own reproduction.

Since the wasp can only attack the full-grown larva of the host, the parasite cannot influence directly the host population while it is in any stage from adult to matured larva. The initial density of the host is determined by the effect of the final density of the host in the previous generation and not by the amount of parasitism. Because the final density of the host in one generation determines the initial host density in the next, the reproductive rate of the host does not take a constant value but varies with the change of host density.

The population density, in the equilibrium state, has the same magnitude in any successive generation. Thus, it can be represented graphically, as in figure 3, at the point of intersection of the curve, representing the relation between the initial and final host densities and the straight line (broken line A in figure 3), which passes through the origin with a slope of 45°. In a population of the host only, the equilibrium value is about 250. With the introduction of a parasite species, however, the equilibrium state moves to another density. This displacement of the steady density is regulated by the action of the parasite or the rate of parasitisation. This varies with the physical factors, such as temperature, humidity, etc., and with the biotic factors, such as host density, parasite density, etc., of the environment.

In a previous experiment (Utida, '43), the number of parasites which emerge in a given generation varies, as is indicated in figure 3, in a definite manner with change in the density of the parasite adults in the previous generation. The final density of the host was 32 and the initial density in a succeeding generation was 350, when the environmental conditions were the same as in the present experiment. The density of the parasites, when they are in the steady state, can be obtained from figure 3. This is done by noting the point of intersection of the curve, which relates parent-progeny density of the parasites, and the straight line which passes through the origin with a slope of 45°. The parasite density, in a state of equilibrium, has a value of 240.

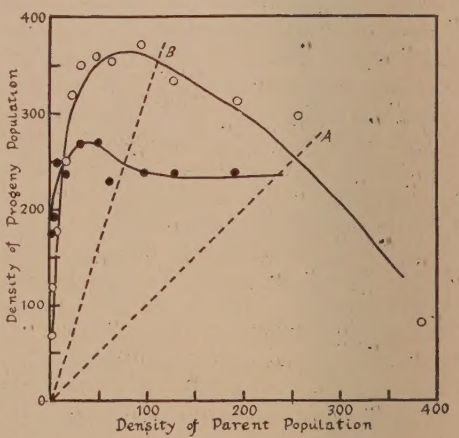

FIG. 3. Relation between the parent density and the density of its progeny in the host and parasite populations. Host population (○), Parasite population (●).

TABLE V. *Obtained values for the level of an equilibrium state and the values calculated for it*

	Obtained experimentally		Calculated
	Population A	Population B	
Initial density of the hosts	349.3	367.1	350
Final density of the hosts	118.9	121.8	120
Density of the parasites	230.4	245.3	245

The amount of parasitism is 68.6 per cent (240/350). It should be noted that this method of estimating the density is valid only when the given environment is saturated with the host population because the reproductive rate of the parasite does not vary when the host density is very high (Utida, '43a).

In the present case, however, the given environment is not saturated with the host population. Sixty-eight per cent of the initial density of the host is parasitized while 31.4 per cent of the host emerges as the final density of the host. To obtain a graph for the relationship between the initial and final host densities (when 31.4 per cent of the hosts are not parasitized), find the point of intersection between the curve, which represents the effect of host density on its own reproduction, and a straight line (broken line B in figure 3), passing through the origin, with a slope of 17 degrees (0.314 = tangent 17°). With this point of intersection, 350 on the x axis, which is the value of the initial host density, gives a value of 110 on the y axis, which represents the final host density. Therefore the steady state of the parasites is 240 (350–110). As is shown in table V, the values obtained experimentally accord closely with the calculated values. This close accord warrants the present method of estimation, which takes account of the effect of host density upon its own reproduction.

DISCUSSION

It has been supposed by many that the position of an equilibrium state is produced by the effects of parasite density and of host density. It has been proved, in a population of the azuki bean weevil alone, that the mechanism which determines the position of equilibrium and causes a regular fluctuation of density is the effect of weevil density itself. Regardless of host-parasite interaction, the establishment of the steady state in a population and the fluctuation of population density are dependent upon the effect of host density.

Nicholson ('33) has reached the conclusion, theoretically, that the equilibrium state is caused by host-parasite interaction, and that the position of this state is determined by competition, i.e. intraspecific competition in a narrow sense. The density effect is a sort of intraspecific competition and they are synonymous. Therefore, the conclusion obtained here corresponds closely to Nicholson's opinion. It differs, however, on the point that Nicholson has stressed the intraspecific competition of the parasite individuals for the determination of the position of an equilibrium state, while the present author emphasizes the density effect of the host population. It may be a great fault in Nicholson's theory that no consideration had been paid to the density effect of a host population as a cause of fluctuation in population density.

To estimate the effect of parasitism, it is well to know the degree of reduction in the level of a host population, when parasites are introduced into the host population. But this is not practical, for the level to which a host population is free from the action of parasites can hardly be seen under usual conditions. In practice, the effect must be estimated by comparing the initial density of the host and the final density of the host, when both the host and the parasite populations are in an equilibrium state.

In the present case, the initial density of hosts is 350 to 370, the final density of hosts is 120 and the rate of parasitism is about 60–70 per cent. The wasp, *Neocatolaccus,* is a parasite attacking the full-

grown larvae of the hosts, which severely damage the bean. The end result of this parasite introduction is fruitless from the standpoint of pest control. Biological control is better when the earlier stages of the host are attacked. The egg stage is the best. But, even if the stadium attacked by the parasite is later than that which causes the damage, it is efficient since the rate of host reproduction is inhibited by the reduction of the final host density. This idea is advanced as a guiding principle of biological control by Marchal ('08) and other followers. According to this opinion, it is logical that the number of deposited eggs decreases by the reduction of the final density of the parent hosts and therefore the initial density of the hosts decreases. Even if it is so, it cannot be known how high the density will be in the following generation. The efficiency of parasitism must also be estimated by the level of density at the equilibrium position. By the graphical calculation mentioned above (fig. 3), it is observed that the host density at an equilibrium state is 250, when the host population is free from the parasite attack; while it is 350, when the host population is attacked by the parasite.

This result is unexpected. The density of the weevil, when it is in the stage which feeds upon the bean, is high when the host population is attacked by the parasite, and it is low when the host population is free from the parasite. This result is not strange if we consider the fact that the effect of density itself is always operative, controlling the population growth.

The parasite reduces the final density of the hosts and the influence of density decreases. Then the rate of reproduction of the host weevil increases owing to the decline in the density effect. This result may not be expected, when the rate of parasitism is high and the point of intersection of the curve, representing the density effect, and the straight line, representing the rate of parasitism, is situated at the left side of a peak indicating the number of emerged weevils, and the growth of the host population is restricted by the action of the parasites.

Nicholson ('33) has not reached the same conclusion on the interaction of a host and its parasite, since he assumed that competition acts between parasite individuals and not in a host population. But, his statement on parasitism, when several parasites attack a common host, is like the present one. When a new specific parasite species is introduced to attack a host species that is already attacked by other specific parasites, the density of the host, at the stage attacked by the introduced parasite, is increased. Comparing them, the action of the parasite already in existence corresponds to the density effect of the host weevil, the action of the newly introduced parasite corresponds to the influences of parasite to host, and the density of the host at the stage attacked by the introduced parasite corresponds to the initial density of the host.

Summary

It is the main point of the present work to verify experimentally, whether or not a host-parasite interaction, under constant conditions, causes a fluctuation in population density. Two series of mixed populations of two interacting species, a host insect, the azuki bean weevil *Callosobruchus chinensis,* and its parasitic wasp, *Neocatolaccus mamezophagus,* were kept under favorable and constant conditions. A count of the number of individuals in the two populations was made every week for a period of 3 years, covering 51 generations of the host.

The densities of both parasite and host populations fluctuated from generation to generation. It is shown that these fluctuations are not caused by any environmental factor of physical nature, but are caused by the host-parasite interaction. These fluctuations do not belong to the true periodic fluctuations, but belong to the so-called cyclic phenomena, which fluctuate with variable periods having a certain definite mean value. These are

not the classical fluctuations of the Lotka-Volterra type, representing the prey-predator interrelation. By applying statistical methods of periodic analysis, for 3, 4, 5 or 6 generations, there were found to be reliable values for a period in both the host and parasite populations.

By calculating the correlation coefficient between the initial and final densities of the hosts and the parasite density in each generation, the following relations were found. The emerging number of wasps is determined by the initial density of host weevils, which relates closely to the final density of the hosts in the previous generation, and the number of wasps determines also the final density of the hosts in a generation.

By applying statistical analysis to the data obtained for the fluctuation, it has been shown that the equilibrium state of population, in the sense of Nicholson's interpretation, actually exists in both host and parasite populations and his interpretation is not a mere supposition. As to the determination of the host and parasite densities at the equilibrium state, the so-called density effect plays an important role.

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VEGETATION AND SOIL RELATIONS IN THE LOWER COLORADO DESERT

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INTRODUCTION

This paper is a study of the relationship between certain plants and plant communities in the Lower Colorado desert and the soils on which they grow. It is not a complete description of this desert's vegetation nor of its soils. Only the commoner plants and plant communities are considered, and there was only reconnaissance work done in the mountains and mountain valleys which form the rugged ribs of the desert. Chemical and mineralogical characteristics of the soils were ignored for all practical purposes, the better to concentrate on possible vegetational correlations with salinity, pH, and moisture-holding capacity.

The first definitive work on the vegetation of this extremely dry region was that of the workers at the Desert Laboratory of the Carnegie Institute at Tucson. Livingston, in his evaporation studies ('06), approached the desert vegetation from the physiological point of view while demonstrating that even in this desiccating climate considerable stores of plant moisture may remain in the soil. Spalding ('09) described the plant communities about the Desert Laboratory and linked them with soil types and exposures. Finally Cannon ('11), in his root studies, showed soil differences in the various desert environments and linked plant distribution with root structures and adaptations.

The most exhaustive work on soils and vegetation in this region is that of Shantz and Piemeisel ('25) which included a considerable area in California, Nevada, and Arizona. Vegetation typical of the Arizona succulent desert, the Colorado microphyll, the Mohave, and the California microphyll deserts, as well as considerable mountain areas of varying vegetation, is included in the area treated by this 1925 paper. Both the intensively studied areas of the Shantz-Piemeisel investigation, the Coachella Valley and the upper Gila Valley, are outside the borders of the desert considered in this present paper. Parish ('14) sketched the vegetation of the Coachella Valley and the borders of the Salton Sea without any special reference to soil types or characteristics.

The botanical nomenclature in the present study follows Kearney and Peebles ('42). The unpublished work of Hendrixson ('40) was useful in the study made of Yuma Mesa.

The writer is indebted to Mr. Maurice N. Langley and to Mr. Samuel B. Watkins, both of the United States Bureau of Reclamation at Yuma, Arizona, for the photographs which illustrate this article and to Miss Annetta Carter of the University of California herbarium at Berkeley for the opportunity of comparing collected plant materials with the specimens there.

These observations were made while the writer was employed as a soil scientist by the United States Bureau of Reclamation in its classification of land for irrigation purposes. Soil and related land studies were the primary basis of this classification program in the course of which extensive data were collected on the salinity, pH, permeability, and moisture-holding capacity of desert soils. A statistical summary of the results of these analyses is given in a separate section.

Within the Lower Colorado desert, a number of specific areas were observed. Most work was done within the Wellton-Mohawk Division of the Gila Project in Arizona and on the West Mesa of the Imperial Division of the All-American Canal System in California. In addition, a number of observations were made on

the Yuma Mesa, Pilot Knob Mesa, and in the Gila, Colorado and Imperial Valleys.

Description of Area

Location

The area discussed in this paper has been variously included in the "Colorado Desert," the "California Microphyll Desert," and so on. It is called the Lower Colorado desert here to distinguish it from desert regions along the Colorado from the Grand Canyon down to Blythe.

The extent of this desert is indicated in the accompanying map (fig. 1). Boundaries, particularly to the north and east, have to be fairly arbitrary. On the west the Laguna and Santa Rosa Mountains form a logical limit, and the Mexican border neatly cuts a natural region which actually continues well on down along the Gulf of California. To the north the Riverside county line cuts off parts of the Salton Sea geosyncline which are more closely related to more northern desert regions, and the Chocolate, the Laguna, and the Castle Dome Mountains represent regions which are topographically distinct from this desert. Finally, the Mohawk Mountains can be used as an eastern boundary, although once the Gila Mountains have been traversed the country is in rapid transition to the Arizona succulent desert which dominates the south central portion of that state.

Climate

The climate of this Lower Colorado desert, summarized in table I, is typical of the extreme desert areas of the southwestern United States. It has low rainfall (around 2.5 to 4.0 inches) combined with extremely high summer temperatures (maxima around 120° F) and the highest percentage (over 90 per cent) of possible sunshine in the United States. The relative humidity is extremely low with an annual afternoon average of 26 per cent at Yuma. Data on wind velocities are not available, but late winter and spring are often extremely windy in this region.

All these factors, it will be noted, are

Fig. 1. Map of the Lower Colorado Desert.

TABLE I. *Climatic data from stations in the Lower Colorado Desert From Smith ('45) and U. S. Dept. of Agriculture ('41)*

Station	Mean temp. Deg. F		Temperature		Growing season (days)	Per cent of possible sunshine	Average precipitation (inches)											
	Max.	Min.	Max.	Min.			Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Imperial	53.6	91.9	124	16	311		.26	.89	.19	.18	.03	.00	.12	.29	.22	.26	.13	.78	3.35
Calexico	53.2	89.8	117	21	311		.49	.52	.29	.08	.06	.01	.09	.57	.24	.17	.29	.37	3.18
Brawley	52.7	91.1	121	19	303		.35	.41	.20	.15	.06	.01	.06	.16	.08	.27	.12	.56	2.43
Yuma Valley	50.8	87.0	117	14	267	90.4	.35	.52	.14	.18	T	.01	.16	.34	.79	.44	.08	.40	3.41
Yuma Mesa	53.5	91.1	118	19	326		.30	.30	.19	.16	T	T	.24	.59	.80	.41	.15	.68	3.82
Wellton	50.9	91.6	120	16	254		.39	.49	.32	.12	.05	.01	.40	.72	.64	.35	.19	.95	4.63
Mohawk	54.5	94.7	126	16	333		.39	.47	.32	.12	.03	.06	.36	.84	.42	.26	.24	.66	4.17

such as to cause extreme desiccation in the plant, so that water supply and adaptations to water loss are the governing ecological factors in this desert.

The rainfall regime shows two pronounced maxima separated by dry periods during which the vegetation quickly becomes dormant. The wet seasons occur in the winter (December, January, February) and in the summer (August, September, October). These two peaks of moisture supply give rise to the two distinct groups of winter and summer annuals.

The diurnal range (around 30° F) and the annual range (around 100° F) are both extremely wide. Related to this is the long growing season which varies from around 250 to around 325 days, according to the location.

Within this desert certain climatic gradients appear. In drawing farther west into the climatic shadow of the mountains of Southern California annual rainfall decreases from over 4.0 inches at Mohawk to less than 2.5 at Brawley. In general, there is probably a tendency for rainfall to increase with elevation but, since all the weather stations in this desert fall within a rather limited range of elevations, this is hard to demonstrate.

Extremely important but poorly investigated are the differences in microclimates within this desert. At Yuma, where stations have been maintained on both valley and mesa, the lower valley lands are perceptibly cooler than the mesa (mean annual difference almost 3° F) and have an appreciably shortened growing season.

Physiography

Physiographically this desert has been determined by two factors. First came the regional mountain building which shoved up the ranges of block-faulted mountains trending northwest to southeast across the desert and warped down the huge trough of the Imperial Valley. Into this mountain-wrinkled region the second factor, the Colorado River, poured its nearly limitless supply of sediments

which were to cut off the Salton Sink and Imperial Valley from the waters of the Gulf. Local erosion and deposition, both by rain and wind, have worked these original formations until the present topography has been produced.

For all practical purposes, the desert can be divided into four physiographic provinces, each one of which has characteristically distinct vegetation on distinct soil types.

The valleys are the lowest in elevation and the richest in vegetation types. Within this desert the tremendous Imperial Valley, the Colorado bottomlands, and those of the now dry Gila River are prime examples of this valley type. Soils are all of recent deposition, uniform within the strata, and with little visible development. In the Imperial Valley the Imperial, Holtville, Meloland, and Niland are the principal series mapped while in the Colorado and Gila Valleys the Gila series predominates; although locally there are clayey or sandy soils, silty soils predominate. In general, the sandy soils and those which present a shallow layer of silt over sand become more frequent as the rivers are approached. On the higher terraces and in the great sink of the Imperial Valley the heavier soils prevail.

Above this alluvial province lie the gently sloping mesas which dominate most of the desert area. It is from the mesas that the valleys have been carved, but the former themselves probably represent a base level of deposition in another erosion cycle. The earth materials which compose the mesas have been derived from the wandering Colorado River and from the washes which course down the sides of the desert ranges after the infrequent downpours of rain. This mixed alluvial-colluvial material is predominantly sandy but it will be found to vary toward a gravelly type nearer the mountains and often toward a more fine-textured type toward the valleys. Wind has worked this water-transported material so that hummocks are an almost universal feature of the mesas, and in places (most notably in a belt which separates Imperial Valley's East Mesa from the Pilot Knob Mesa) sizeable sand dunes have been formed. Two soil series are predominant on the mesas. The Superstition series is formed on coarse water-deposited sands while the Rositas occurs on the finer wind-worked deposits. On the higher mesas where alluvial fans predominate a more developed soil, the Whitlock, is frequent.

Above the mesas but virtually indistinguishable from them are the mountain pediments or bajadas. These are plane areas of considerable slope cut by occasional washes. The bajada province is distinguished by the fact that here a balance has been struck between erosion and deposition. Here soils, principally of the Mohave and Tijeras series, developed from either transported or residual materials, are older and show more distinct development than any other soils of the region. Texturally the soils are gravelly, but finer materials are not absent. Cementation of the subsoil is almost universal.

The mountains appear in this area mostly as boundaries, but there is no spot in the Lower Colorado Desert where there are not mountains visible on several horizons. Block faulting and the attendant vulcanism made most of them and scattered them in parallel lines through the desert. Typically the mountains have a core of granite, gneiss, or other plutonic rocks, coupled sometimes with conglomerates of fairly recent date, while along the fault lines at the mountain edges cinder cones of volcanic tuff appear. The valleys within the mountains are floored with colluvial material washed down from the mountains themselves.

Description of Communities

The Lower Colorado Desert falls within the area included in Clements's desert scrub formation. Under Merriam's classification (1898) the bulk of it would be in the Lower Sonoran life-zone although Merriam's maps show ribbons of the Tropical life-zone extending up the valleys

of the Colorado and Gila. It is the writer's view that, contrasting though they may be, the valley and mesa vegetative groups are similar enough to be considered one formation, and in this paper they will be treated as such.

Valley Communities

Owing to the wide variability of soils and moisture the valley communities show the greatest variation of any of the vegetation groups in this desert. The soils may vary from clays to clean sands or from salt-free to heavily saline, and the water table may be only a few feet from the surface or far below the reach of plants.

Pluchea-Tamarix community.—In the lowest bottomlands is a characteristic community which produces the most abundant and varied vegetation of any in this desert. In clear and continuous lines paralleling the channels of the rivers and dropping into old oxbows, the dense thickets of *Pluchea sericea* (arrowweed) and *Tamarix gallica* (salt cedar) mark this zone quite plainly (fig. 2). Both of the two dominants are dependent upon underground water and virtually independent of soil texture. They will never be found on the upper terraces, nor will they be found where the water table is far below the surface. It is interesting to note Cannon's ('11) soil moisture findings in valley soils near Tucson. From 8 inches to 17 feet he found 13 to 23 per cent of moisture much of it readily available to plants. Underground moisture is controlling in this community's distribution. Thus it is that far from the river channels this river bottom community often appears beside an irrigation ditch.

In habit this community resembles first bottom communities of more temperate

FIG. 2. View of the Gila River bottomlands northwest of Dome. *Pluchea-Tamarix* community. The soil here is variable; both sand and silt can be seen exposed in the cut bank and above it. The light-colored shrubs in the immediate foreground are *Atriplex lentiformis*. Behind them the bottomlands are densely covered with the light-colored *Tamarix* and the darker *Pluchea*. *Populus fremontii* is the lone tree visible in the right distance.

river valleys. The *Pluchea* is reminiscent in its erect and rank growth of *Ambrosia trifida,* while the *Tamarix* mimics the habit of some of the shrubby *Salix* spp.

This community is rich in species as well as in individuals. Here *Prosopis odorata* (screwbean) forms thickets and *Baccharis glutinosa* is locally abundant enough to replace one of the other of the co-dominants. *Atriplex lentiformis* (big saltbush) is often rather luxuriant and *Aster spinosus* is another species which may become locally conspicuous, particularly where the soil is slightly saline. Along the river channels *Salix gooddingii* (black willow) and *Populus fremontii* (cottonwood) mark the course where water has flowed.

It should be emphasized that this association is almost completely independent of soil textures. If subsurface moisture is present it can be found on everything from silty clay loams to clean sands, on shallow soils (i.e. soils showing silty textures at the surface but underlain at shallow depths by sand or gravel) and on deep ones. The overwhelming majority of sites where this community is found shows non-saline soils (average of 140 samples under both *Pluchea* and *Tamarix* shows 0.14 per cent salinity). Still, there are enough cases where *Pluchea* and *Tamarix* grow on saline soils to show that neither is intolerant of salt, so long as moisture is present and available for plant growth.

Prosopis community.—Just above the lowest bottoms is the most conspicuous valley community, that dominated by *Prosopis juliflora* var. *glandulosa* (mesquite) (fig. 3). Nichol ('43) classifies all valley lands as "mesquite bosque" and before settlement this was probably by far the most predominant of the valley communities. These channel mesquite may be grouped in dense orchard-like groves or they may be more scattered. In habit they are reminiscent of the bottomland species of *Craetegus* of more humid regions.

The original extent of this community has been reduced by a number of factors. The Cocopahs and Yumas had found a multitude of uses for the wood and the early settlers discovered that under the mesquite they could be fairly certain to find deep soil of medium texture, eminently suitable for irrigated farming. Lately the steady lowering of the water table attendant upon pumping in the Gila Valley has doubtless accounted for considerable mortality among the formerly vigorous trees, for deep-rooted as the mesquite may be, there are probably very few individuals with roots extending more than 25 feet down from the base of the trunk.

The present-day remnants of the mesquite community are most common along the Gila River, for it is there that the smallest proportion of valley land has been placed under cultivation.

In the field the mesquite is occasionally found very nearly as a monotype, but more commonly it is associated with one or both of two shrubs, *Suaeda torreyana* (inkweed) and *Atriplex polycarpa* (desert saltbush). In general, the predominance of the *Suaeda* indicates a more saline condition (an average of 131 samples showing 0.90 per cent salinity) than when the *Atriplex* is the chief companion of the *Prosopis* (average of 250 samples showing 0.42 per cent salinity).

Aside from the salinity, which may in areas present a considerable problem, lands under this mesquite community are usually preeminently suited for irrigated farming. They are usually medium textured, ranging from very fine sandy loams to silty clay loams, and drainage is unrestricted. It has been largely this indicator quality of the *Prosopis* community which has led to its destruction in favor of agriculture.

Atriplex community.—Interspersed in the Prosopis, or sometimes in a belt between it and the higher mesas, lies a community dominated by species of *Atriplex* (fig. 4). Except for the absence of sod, this community has much the aspect of the sagebrush-dotted western Great Plains. The shrubs are evidently spaced for maxi-

FIG. 3. *Prosopis juliflora* var. *glandulosa* near Wellton. The tree in the center is conspicuously parasitized by *Phoradendron californicum*.

FIG. 4. *Atriplex polycarpa* community near Wellton.

mum occupance under the scant rainfall, but there are wide, empty gaps between individuals.

In the Arizona portion of the desert it is *Atriplex polycarpa* which is most frequently encountered, while in California's Imperial Valley *A. linearis* (narrowleaf saltbush) is more frequent. Other *Atriplices* such as *A. canescens* (chamiso) and *A. lentiformis* may appear in this community but they are not typical. *A. canescens* is characteristically a plant of sandy soils while *A. lentiformis* prefers the lower, moister bottoms. Shrubs of other genera may appear. *Lycium andersonii* (desert-thorn) is not uncommon, particularly in the heavier soils. On lighter soils and where this community is in transition to those more typical of the mesas, *Larrea tridentata* (creosotebush) is a common associate.

The *Atriplex* community seems to favor the upper terraces of the river valleys. It will not be found in the first and second bottoms of the river, nor will it be found above on the sandy mesas. It is on the older, relatively heavy-textured (silt loams to silty clay loams) soils in between that it will be found. Evidently soil development has something to do with this distribution for characteristically the soil under the *Atriplex* community, though alluvial in origin, shows already the pinkish tinge which comes with development of desert soil. Like the *Prosopis* community, this *Atriplex* community is usually, though not invariably, an indicator of medium-textured soil without excessive salt accumulation. A group of 35 samples averaged 0.11 per cent salinity. Soils under this community are probably best suited to agriculture of any in the desert.

Saline communities.—Saline soils in the valleys are plainly indicated by another community with two distinct faciations. *Suaeda torreyana* in dense stands (fig. 5) indicates moderate salinity (0.2–1.0 per cent) of medium or heavy-textured soils, much as it indicates salinity when associated with *Prosopis*. On these moder-

FIG. 5. Salt shrubs near Dome. In the foreground *Allenrolfea* occupies the center of a salt spot. The dense *Suaeda* in the background marks the edge of the spot.

ately saline soils it may occur alone or accompanied by *Lycium andersonii* or *Atriplex linearis*. The other faciation of this saline community is dominated by abundant *Allenrolfea occidentalis* (pickleweed) which often grows densely on the moist saline soil to the exclusion of all other species. The soil difference between the *Suaeda* and *Allenrolfea* faciations seems to be that the *Suaeda* indicates saline surface soil, while the deeper-rooted *Allenrolfea* shows salinity throughout the soil profile. The relationship of the two is reminiscent of that of *Distichlis spicata* which indicates salinity in moister regions and *Sarcobatus vermiculatus* which shows subsoil salt. Thus surface soils under 46 *Suaeda* sites show 0.56 per cent of soluble salts, while the subsoils average 0.40 per cent of salinity. Under 35 *Allenrolfea* sites the corresponding figures were 1.91 per cent and 1.92 per cent. *Allenrolfea* is invariably an indicator of heavy-textured soil, ranging from the heavier silt loams to the clays, and these soils are invariably deep ones.

Sand communities.—Within the complex of heavier soils old river channels and adjacent dune areas have their characteristic sand-loving communities. *Larrea tridentata* and *Atriplex canescens* are characteristic of these valley sand areas, particularly the windblown ones, and where the sand lies low enough *Pluchea sericea* and *Tamarix gallica* are also found. Still it is not the woody plants which characterize these sandy areas best; often they are large barrens clothed only by herbs characteristic of sandy soils.

The windblown areas of loamy sands with only moderately low water-holding capacity are characterized by two herbs, *Palafoxia linearis* and *Petalonyx thurberi* (sandpaper plant). Under 9 sites where *Palafoxia* grew the first 4 feet of soil held an average of 4.1 inches of plant-available water (see section on "Methods") at field capacity.

In the clean sands of the river bottoms and in old abandoned river channels a more extreme sand condition is indicated by *Dicoria canescens* and *Coldenia plicata* which alone clothe the sand barrens. Under this community plant-available water which can be held in the first 4 feet of the sand is probably less than 2 inches.

Heavy soil communities.—At the opposite end of the textural spectrum from the sands are the heavy soils, the clays and clay loams, which exist in many basins in the valleys. The early soil surveyors called this type "Salt River Adobe." Often these heavy soils are associated with saline areas and then the usual saline indicators are dominant, but there are many places where these areas of heavy soils and impaired drainage are free from excessive salinity.

Tamarix gallica is the principal woody plant of the clay basins wherever the subsoil moisture is present. While *Pluchea sericea* is entirely confined to light or medium-textured soils (sands to silty clay loams), the *Tamarix* readily moves into the clay wallows left by a retreating river.

There are some fairly large clay areas clothed only by herbs. *Actinea odorata* is perhaps the most abundant species on these poorly drained soils, but the luxuriant *Datura metelioides* is abundant here too. *Teucrium depressum* and the ill-smelling *Petunia parviflora* are occasionally found in dense societies in these basins. Small, heavy-soiled drainageways show plant societies of similar composition. Here in addition are found *Cucurbita palmata* (coyote melon) and *Nicotiana trigonophylla* and *N. clevelandii*.

Weed successions.—On cultivated lands in the Mohawk Valley, where pump irrigation has been practiced, weeds indicate the degree to which saline irrigation water has salted up the soil. Small grains and alfalfa are invaded by *Cynodon dactylon* (Bermuda grass) which is still a profitable hay and seed crop. As the salting-up process proceeds, the Bermuda dies out and the more resistant *Polygonum argyrocoleon* comes in abundantly. The final stage is marked by bare soil dotted only with the semi-prostrate *Atriplex semibaccata* (Australian saltgrass) which can

FIG. 6. *Larrea-Atriplex* community in the South Gila Valley. *Atriplex polycarpa* and *Larrea tridentata* are dominant here but in other places will be joined by mesquite. An abundant growth of low annuals is appearing after the winter rains.

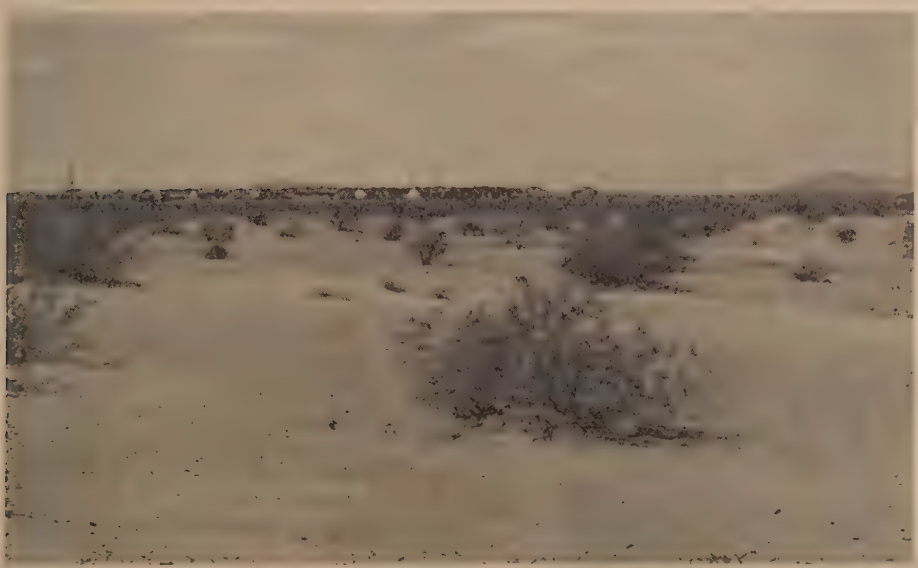

FIG. 7. *Larrea-Franseria* association on the Yuma Mesa. The large shrubs are the *Larrea*, the small, apparently leafless ones the *Franseria*. The soil here is a loamy sand with a moisture-holding capacity of almost 4 inches (see section on methods).

grow in the most saline soil if furnished sufficient moisture.

Mesa communities

Larrea-Atriplex community.—Between the valley communities and the mesas lies a transition region where *Atriplex polycarpa* and *Prosopis juliflora* var. *glandulosa* are mixed with the two mesa dominants, *Larrea tridentata* and *Franseria dumosa* (fig. 6). This is a region of mixed soils, sandy loams and loams grading down to loamy sands. In the Sonora Desert south of the Mexican border below Yuma *Atriplex canescens* replaces *A. polycarpa* in this transition, and about the edges of the Imperial Valley it is usually *A. linearis* which occupies this place, but always, throughout the area, this transition is characterized by a mixture of valley and mesa species. The water-holding capacity of these soils is fairly good. Soil samples from 58 sites averaged 5.2 inches of plant-available water in the top 4 feet. Salinity is usually low; 101 samples averaged 0.19 per cent.

Larrea-Franseria association.—The typical mesa community is the creosotebush-bursage association, the community which covers more area in this Lower Colorado Desert than any other. To all intents and purposes, this *is* the desert scrub formation.

Larrea is the ubiquitous shrub of the desert. It is every place in all four physiographic provinces, on almost every kind of soil. Spalding's ('09) comment is to the point:

> "It is impossible to enumerate completely the peculiarities of this plant, structural and physiological, which have enabled it, more successfully than any other, to cope with the worst of desert conditions, as they exist in the Southwest."

The *Larrea-Franseria* association (fig. 7) resembles only itself. It consists of widely scattered individuals of *Larrea*—in this arid environment the condition of maximum occupancy—with bursage checkering the intervening spaces. Through most of the year this community is barren. Then, after the rainy seasons, many annuals rapidly appear to fill the blank spaces between the scattered *Larrea* before disappearing just as suddenly as they came. Interesting as the annuals are, they are an ephemeral feature of the mesa's aspect, apparently without any indicator significance for soils. They are, therefore, omitted from this discussion.

The typically balanced mesa association can vary in three directions. It can approach the gravelly washes of the mountain province, it can vary toward areas of blowsand, or it can vary toward heavier soils. Changes in all directions are marked by the intrusion of other species into the dominant matrix of the *Larrea-Franseria* association.

Gravelly mesa types.—The first stage in the transition toward gravelly soil is marked by the entry of *Opuntia leptocaulis* (Christmas cholla) which appears most abundantly on the mesas east of the Gila Mountains. Farther west it is replaced on similar soils by *Croton californicus* which on the West Mesa of Imperial Valley is the first indicator of gravelly soil. In both places *Krameria grayi* (crimsonbeak) is associated with this degree of gravel.

In looser gravels under more pronounced wash conditions, other species appear. In the eastern portion of this desert three leguminous trees, *Acacia greggii* (catsclaw), *Olneya tesota* (ironwood), and *Cercidium floridum* (palo verde), join with the Arizonan *Cereus giganteus* (saguaro) (fig. 8) to indicate land much too gravelly ever to be used in agriculture. The *Cereus* reaches its approximate western limit at the Colorado River while the three legumes are not very widespread beyond the sand dunes which form a barrier belt between the Chocolate Mountains and East Mesa. On the California portion of the desert it is the bare-branched *Dalea spinosa* (smoketree) and the related *D. schottii* which definitely indicate these pronouncedly gravelly soiis. Two herbs, *Encelia frutescens* and *Bebbia*

FIG. 8. A wash on the bajada with Mohawk Mountains in the background. *Cereus giganteus, Olneya tesota,* and *Cercidium floridum* in the gravelly wash. *Larrea* and *Franseria* in the foreground.

juncea var. *aspera,* are usually found in these extremely gravelly mesa areas.

Sandy mesa types.—Although all the mesas are sandy to some degree, there are portions where wind or water action has accumulated purer or "cleaner" sands. These sandy areas occur on all the true mesas (counting the Pilot Knob Mesa as a bajada area), but there are usually localizations, such as the sand dune region toward the Mexican border on the Yuma Mesa and the sand hills which separate Pilot Knob Mesa from the East Mesa of Imperial Valley.

There is great variability within this desert in sand vegetation. There is, for instance, the sand-loving *Dalea emoryi* which is very nearly confined in its range to this Lower Colorado Desert. East of the Gila mountains this *Dalea* is found only on extremely sandy soils, lands which could not be used in any case for irrigation. Moving westward to the Yuma Mesa, the *Dalea* appears on lands of borderline arability and, by the time the dry stretches of West Mesa are reached, the *Dalea* appears on all lands from loamy sands to coarse sands.

The appearance of *Hilaria rigida* (galleta) is usually a good indicator of increasingly sandy soils (fig. 9). When this is coupled with *Dalea emoryi* and *Coldenia palmeri* the observer can assume that the fine materials are disappearing from the sandy soil. The very poorest sands from an agronomic point of view are those occupied by *Ephedra trifurca* (Mormon tea) and by *Eriogonum deserticola* Wats. In general, the progression from the sandy loams to the poorest sands is something as follows: On the sandy loams *Larrea* and *Franseria* grow to the practical exclusion of all other perennials. In the loamy sands to sands *Hilaria* appears followed soon by the *Dalea. Larrea* decreases on these poorer quality sands, but the *Franseria* holds its own beyond the loamy stage. *Coldenia palmeri* marks a further decrease of the water-holding capacity of the sand, but the final step into coarse clean sand is marked by the dominance of *Ephedra* and *Eriogonum.* On

FIG. 9. *Larrea-Franseria* association on Yuma Mesa. These are poor lands of nearly clean sand. Here the *Larrea* is much sparser than the *Franseria*. Some *Hilaria rigida* appears on the hummocks.

the poorest land the *Franseria* disappears.

It is worth noting, in passing, that many sand dunes of moderate water-holding capacity (about 2 to 3 inches of plant available water in the upper 4 feet) are covered with robust individuals of *Larrea*. This species may occupy the areas to the virtual exclusion of all other vegetation except on some hummocks where accumulated fine material allows mesquite to grow prostrate. This is the same species and variety, *Prosopis juliflora* var. *glandulosa*, as the sturdy channel mesquite, but in this environment it has descended from a tree to a scraggly shrub barely sprouting above the accumulating sand and dust.

Heavy soil mesas.—The *Larrea-Franseria* association can vary toward a heavy soil type, and it does so not infrequently on the Wellton-Mohawk (fig. 10) and the West Mesas. East of the Gila Mountains this change usually brings with it the appearance of *Atriplex polycarpa*, but on the California mesas it is *A. linearis* which comes in. As the soil becomes heavier—toward the silty clay loams and silty clays—the *Franseria* disappears and the *Larrea*, now straggly and depauperate, remains with only an occasional *Atriplex*. On the clays, vegetation, except for a few stunted individuals of *Larrea*, is entirely lacking. Many of these heavy soils are extremely saline and the presence of *Larrea* here belies the frequent citing of this shrub as an indicator of salt-free soils.

Mesa-valley contrast.—It is interesting to compare the mesa and valley environments. The differences are probably not due to soil texture, since both mesa and valley have wide textural ranges within their boundaries. Yet, from the descriptions above, it can be seen that valley and mesa communities contrast sharply. Even species, such as *Prosopis*, which enter both provinces, show the contrast in their divergent habit in the two environments. There are some pairs of closely related

species preferring similar soil textures which neatly separate between valley and mesa. *Coldenia plicata* and *C. palmeri* are both abundant plants of sandy soils but the first is confined to the valley while the second is found only on the mesas. *Dalea parryi* is not uncommon in the valleys where it occupies much the same sites that *D. emoryi* occupies on the mesas. Some factor, possibly micro-climates or a chemical factor related to soil development, has made the mesa environment distinctly different from that of the valley.

Bajada communities

The bajadas show no marked change from the mesas. They are, in fact, usually lumped in with the mesas in regional descriptions and one "mesa," the Pilot Knob Mesa, is actually a bajada area.

The *Larrea* and *Franseria* characteristic of the mesa are still present on the bajada, but they are much more widely scattered and have been joined by new species. *Hilaria rigida* is abundant in washy parts of the bajada and toward the east a number of cacti such as *Opuntia ramosissima, O. leptocaulis, O. basilaris, O. bigelovii* and *Echinocactus acanthodes* appear in this province. Most characteristic is the graceful *Fouquieria splendens* (ocotillo) (fig. 11) which grows throughout the desert on the bajadas. *Fouquieria* indicates a gravelly soil with considerable cementation and some fine materials among the coarse. It will not be found on the most gravelly of the bajadas. At 18 sites under ocotillo the soil would hold an average of 5.3 inches of water in the first 4 feet.

On the most gravelly of the bajadas it is *Atriplex hymenelytra* (desert holly) which serves as an indicator along with *Baileya pauciradiata* and *Encelia farinosa* (incienso). In the gravelly washes of the bajada are found many of the characteristic species of the mesa washes together with shrubs like *Tetracoccus hallii* and *Hyptis emoryi.*

Mountain communities

The mountains in this desert do not rise into different life-zones but they are perhaps slightly moister than the other provinces and quite probably have a still hotter climate (see the data from Mohawk in table I). The vegetation has been fully described in other places (see Shreve *in*

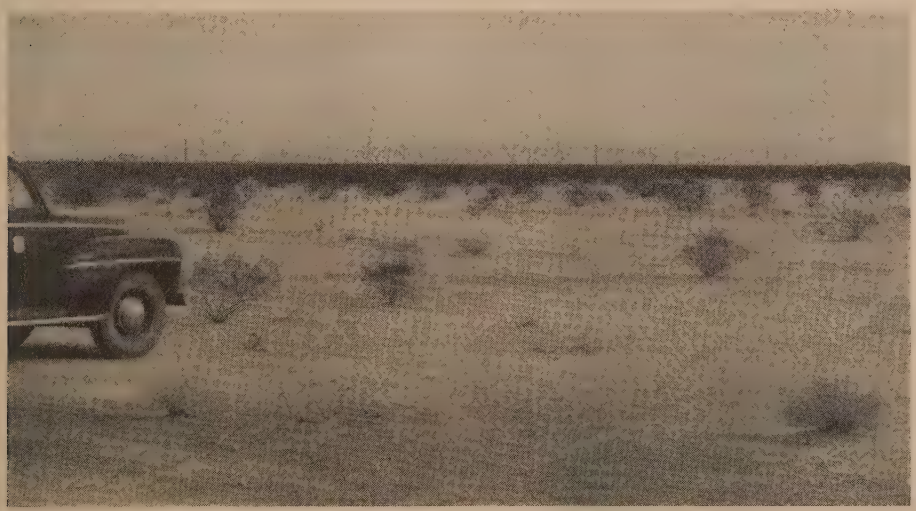

FIG. 10. *Larrea-Franseria* association on the Wellton-Mohawk Mesa. The soil here is a sandy loam, as evidenced by the wider spacing of plants and the sparseness of the *Franseria* in relation to the *Larrea.*

FIG. 11. *Fouquieria splendens* on the bajada near Ligurta. *Larrea, Franseria,* and *Hilaria rigida* are also present.

Kearney and Peebles, '42). No soil studies were made in the mountain province so discussion of them is omitted here.

METHODS

The observations summarized in this paper were made in conjunction with the land classification program of the Bureau of Reclamation in the Lower Colorado District. In going over the lands for classification, test holes were dug to a depth of 4 feet on a grid system of 100 holes to a square mile at rectangular intervals of a tenth of a mile. Vegetation at the site of each test hole was recorded and soil samples were taken of each horizon or stratum occurring in the soil. It will be seen that samples taken on this grid system approximate a random sampling and should be subject to little sampling error.

Samples ranging in texture from sandy loams to clays were tested for salt content and for pH in the laboratory. This was done with the use of a conductivity bridge and the Beckmann pH meter. Sands, loamy sands, and some sandy loams were tested for their ability to hold moisture against the force of gravity. This was done by means of an apparatus fully described by Goodwin and Langley ('46) and Langley ('48). For use in engineering and agronomic work the percentage of moisture was converted to the number of inches of plant-available water which could be held against the force of gravity in the top 4 feet. In sandy soils with a volume weight of around 100 pounds per cubic foot, where about half the water at field capacity is available to plants, inches available in 4 feet may be converted to percentages by dividing by 38.4.

Richardson ('47) working with this apparatus showed an intimate correlation between moisture retention and the percentage of silt and clay found in the soil. Thus if his figures for soils in this area are converted to inches of moisture avail-

able in 4 feet, sands range from 1.0 to 3.7 inches, loamy sands (containing more than 15 per cent silt plus clay) 3.8 to 4.8 inches, and sandy loams can hold more than 5.0 inches of plant-available moisture.

Laboratory Results

The laboratory results for the samples collected and tested as described in the preceding section are summarized in tables II and III. The salt results are particularly interesting with regard to the valley communities while the results on moisture retention are of interest in mesa communities.

In Table II the various communities are arranged in ascending order of salt content as shown by the mean values derived from samples collected from field examples of these communities. Not all differences in means are significant. Thus there is no great difference in soluble salt content of soils under *Atriplex polycarpa* (alone) and that under the *Pluchea* and *Tamarix* of the lower bottoms. If these communities are considered significantly different from the fifth on the list, the *Larrea-Atriplex* community, there is only one chance in 11 of being in error. These first four communities are significantly different from the sixth, which is dominated by *Prosopis,* and the significance of the difference between the *Larrea-Atriplex* community and the *Prosopis* community is near the ten per cent level. There are no significant differences between the *Prosopis*-dominated community and the next three on the list so they can be grouped together. A highly significant difference of means occurs between this group and the *Prosopis-Suaeda* community which occupies the next rung of increasing saltiness. Finally the *Allenrolfea* community is very significantly more salt tolerant than the *Prosopis-Suaeda* type.

Table III. *Plant available moisture in inches in top four feet* (inches × 10)

Dominant species	No. of samples	Mean	Standard deviation
Coldenia palmeri	11	23	7.7
Acacia greggii	8	24	7.8
Olneya-Cercidium	27	31	18.3
Dalea emoryi	12	37	15.8
Palafoxia linearis	9	41	13.4
Opuntia leptocaulis	19	42	17.5
Hilaria rigida	62	46	13.4
Larrea-Atriplex	58	52	11.0
Fouquieria splendens	18	53	8.3

It is interesting to compare differences between top and bottom horizons under *Suaeda* and *Allenrolfea.* The correspondence of top and bottom under *Allenrolfea* is striking. There is a mean difference of 0.16 per cent of soluble salts between top and bottom horizons under *Suaeda.* Analysis shows this difference has three chances out of four of being significant.

The picture with the moisture-retention figures is analogous (see table III). Using Fisher's methods for determining significance in small samples the impor-

Table II. *Soluble salts in soil below selected vegetation types* (% × 100)

Dominant species	No. of samples	Mean	Standard deviation
Atriplex polycarpa	35	11	19.1
Pluchea sericea	173	14	17.6
Pluchea-Tamarix	140	14	21.7
Tamarix gallica	39	16	15.6
Larrea-Atriplex	101	19	27.2
Prosopis juliflora var. *glandulosa*	41	36	66.8
Suaeda torreyana (bottom soil horizon)	60	40	57.6
Prosopis and *Atriplex polycarpa*	250	42	63.9
Suaeda torreyana (top horizon)	46	56	81.6
Prosopis-Suaeda torreyana	131	90	28.0
Allenrolfea occidentalis (top horizon)	35	191	114.2
Allenrolfea occidentalis (bottom horizon)	64	192	90.8

tance of the mean differences can be determined. *Coldenia palmeri* growing on clean, wind-worked sands and *Acacia greggii* in the gravelly washes form a pair at the foot of the moisture-retention scale. *Dalea emoryi, Opuntia leptocaulis,* and *Palafoxia linearis* grow on sites with significantly higher moisture-retention values while the *Olneya-Cercidium* soils fall in a position of doubtful statistical significance between this group and the lowest pair. Highest moisture-retention values are shown under the *Larrea-Atriplex* community and under the *Fouquieria* where the figures differ most significantly from less retentive sites. *Hilaria* occupies an intermediate position of doubtful significance between the *Dalea* and the *Fouquieria* groups. Samples were tested for pH on soil paste in many cases but there were no significant differences which could be correlated with vegetation. In fact, the constancy of the pH within physiographic provinces was almost startling. Valley soils ranged from 8.0 to 8.3 in average pH, mesa soils averaged 8.6, while the transition zones between the two provinces showed a value of around 8.4.

Summary

This is a study of the relationship between plant communities and the soils on which they grow in the Lower Colorado Desert. The observations were made in the course of the classification of lands in that desert by the Bureau of Reclamation.

The climate of the desert is a continental one of extreme aridity, high temperatures, a long growing season, and a wide diurnal and annual temperature range. For the plant the water supply becomes the primary adaptive problem and is the principal ecological factor. Local climates typical of valley, mesa and mountain provinces vary the general picture.

The desert is divided into four physiographic provinces with characteristic soils and vegetation. The valleys have alluvial soils of all textures, many of them saline. The mesas have mixed alluvial-colluvial soils mostly of sandy textures. The bajadas, or mountain pediments, have cemented gravelly or coarse sandy soils of colluvial or residual origins, and the mountains have rough broken lands of residual rock with only pockets of soil development.

The desert is within the region of the desert scrub formation. In the valley four communities are described dominated respectively by *Prosopis,* by *Pluchea* and *Tamarix,* by species of *Atriplex,* and by salt shrubs. The *Prosopis* community has two sub-communities in which the *Prosopis* shares dominance respectively with *Suaeda* and with *Atriplex.* Within the *Pluchea-Tamarix* community are two societies typical respectively of sandy and clayey soils. The salt shrub community includes two subcommunities, one dominated by *Suaeda* and one by *Allenrolfea.* One association, the *Larrea-Franseria,* is described on the mesa, together with its subcommunities, and one community dominated by *Fouquieria* and various cacti is described on the bajada.

Soil samples collected under the communities described were tested for moisture retention, per cent of soluble salts present, and for pH. The *Atriplex* and *Pluchea-Tamarix* communities are the least saline in the valley; the *Prosopis,* the *Suaeda* and the *Prosopis-Atriplex* communities are significantly more saline. The *Prosopis-Suaeda* community is significantly more saline than these, while the *Allenrolfea* community is significantly the most saline of all. Moisture retention figures show soils under *Acacia greggii* and *Coldenia palmeri* as having least moisture-retaining power, soils under *Dalea emoryi* and *Opuntia leptocaulis* significantly higher, while soils under *Fouquieria* and the *Larrea-Atriplex* community have significantly the highest values observed among the sandy soils. No correllations were found between vegetation as such and pH values, although there was a definite relation between pH and physiographic province.

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LIMNOLOGICAL STUDIES IN CONNECTICUT. IX. A QUANTITATIVE RADIOCHEMICAL STUDY OF THE PHOSPHORUS CYCLE IN LINSLEY POND

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Evidence has been presented (Hutchinson, '41) that in small stratified lakes phosphorus is continually passing from the mud to the water and at the same time is being removed from the water by incorporation into the bodies of plankton organisms which sediment when they are turned to faecal pellets or otherwise die. The persistent low concentrations of phosphorus, observed in the surface waters of eutrophic lakes during the summer appear to represent fluctuations around a steady state concentration presumably determined by the rate of liberation of phosphorus from the mud and the rate of sedimentation of sestonic phosphorus. Such a dynamic view of the phosphorus cycle, even at times of extreme thermal stratification, can also be derived from the experimental study of Einsele ('41) published almost simultaneously with that of Hutchinson, but only recently available in this country. Einsele added massive quantities of phosphate to the surface waters of the Schleinsee and found a rapid uptake and rapid sedimentation of this phosphate, so that the lake ultimately returned to its original condition.

Hutchinson and Bowen ('47) demonstrated the sedimentation of phosphorus from the epilimnion into the hypolimnion of Linsley Pond by the use of radiophosphorus. They added approximately 10 mc. of P^{32} in the surface waters of Linsley Pond on June 21, 1946; a week later 47% of the radiophosphorus present in the lake had descended below the 3 m. level and 10% below the 6 m. level, in spite of very stable thermal stratification below three meters throughout the period of the experiment. The present paper describes a second experiment on the same lake, in which the use of larger amounts of radiophosphorus and more sensitive counting equipment have permitted quantitative estimates of the rate of movement of phosphorus in the lake, and have also brought to light certain additional and unexpected features of the cycle of the element.

Description of the Experiment

The experiment was started on the morning of July 25, 1947. During the taking of the temperatures and water samples in the deepest part of the lake the wind was observed to be variable in direction. It was therefore decided to introduce the radiophosphorus in twenty-five portions while rowing in an approximately circular course between the central deep part of the lake and the margin; this arrangement is believed to have provided adequate opportunity for the mixing of the radiophosphorus with the superficial layer of the lake. The radiophosphorus was added as potassium phosphate, one-fifth of an irradiation unit of initial activity 350 mc., from the Clinton Laboratories, Oak Ridge. The quantity of radiophosphorus actually introduced corresponds, on the arbitrary scale employed in presenting the results and explained below, to 1350×10^6 counts per minute.

Temperature curves for the entire period of the experiment are given in figure 1. On August 1 the mercury column of the only available thermometer was found to be sticking badly, so that no reliable readings are available for this date. The only important temperature change observed during the entire period of the experiment was a marked superficial heating prior to and a superficial cooling subsequent to August 15. This change is

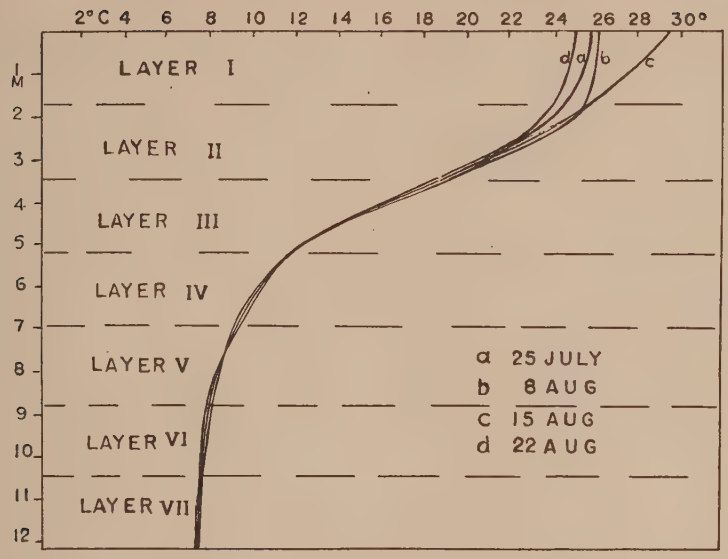

FIG. 1. Distribution of temperatures during the period of the experiment.

probably reflected in the behavior of the phosphorus in the epilimnion in a way subsequently to be discussed.

The samples for analysis and radioactivity determinations were collected in a Nansen bottle lowered on a graduated rope. This rope had originally been marked at meter intervals and then waterproofed in melted paraffin; during the waterproofing it contracted so that it is necessary to correct the depths. This circumstance explains the choice of boundaries for the seven layers into which the lake is divided for the purpose of the experiment. Two samples were collected with the top of the bottle at the top, two at the bottom of each layer, and two at three intermediate depths in each layer. Since the bottle is 54 cm. long, there is a slight overlap between the samples from each intermediate depth and an overlap of about 54 cm. between each layer. This arrangement insures that every horizontal layer in the lake was included in the sampling. It has the slight disadvantage that in any computation based on the sum of several layers, the depth constituting the boundary is overweighted, since it contributes to the bottom of one layer and the top of the layer immediately below it. There is, however, no reason to believe that any serious error is introduced by this procedure. All the samples were taken in the central station in the deepest part of the lake, normally used in our limnological studies of Linsley Pond. Total phosphorus was determined in water samples taken at the time that the temperatures were taken (table I). Since seston phosphorus was determined from the seston samples used for radioactivity determinations, it should be compared with the mean total phosphorus at the top and bottom of each layer (table II). The

TABLE I. *Total phosphorus (mg. per m.³)*

	July 25	Aug. 1	Aug. 8	Aug. 15	Aug. 22
0 m.	16	16	14	19	19
1.75 m.	20	21	21	21	22
3.5 m.	22	22	27	28	34
4.4 m.	—	37	—	—	—
5.3 m.	62	33	50	43	44
7.0 m.	48	53	75	88	82
8.8 m.	140	120	100	150	150
10.5 m.	60(?)	180	160	220	100(?)
12.2 m.	200	240	310	310	360

TABLE II. *Total and seston phosphorus, mean concentrations in each layer: mg. per m.*^{3}

Depths		Aug. 1		Aug. 8	Aug. 15		Aug. 22	
		tot.	sest.	tot.	tot.	sest.	tot.	sest.
I	0–1.75 meters	19	10	18	20	18	21	7
II	1.75–3.5 meters	22	10	24	25	16	28	13
III	3.5–5.3 meters	31	8	39	36	19	39	25
IV	5.3–7.0 meters	46	15	63	66	46	63	21
V	7.0–8.8 meters	87	36	88	119	78	116	41
VI	8.8–10.5 meters	150	50	130	190	67	125(?)	83
VII	10.5–12.2 meters	210	148	240	270	23	230(?)	117

seston phosphorus samples for August 8 were obviously grossly contaminated, possibly due to accidental use of a phosphate-containing cleaner on the glass-ware employed on that date, and have been rejected.

The water samples for radioactivity determinations, coming from five depths at which a Nansen bottle holding 1.25 liters was filled, consisted of approximately 12.5 liters. The samples were filtered through large No. 54 Whatman filter paper using suction from a Cenco Highvac pump. Several changes of paper were required to insure filtration within a reasonable period. The papers (*seston fraction*) were dried and ignited. The filtrates (*filtrate fraction*) were evaporated almost to dryness, oxidized with nitric and perchloric acids; phosphoric acid was then added as a carrier and the phosphorus precipitated as ammonium phosphomolybdate. The ash of each seston fraction and the phosphomolybdate precipitate of each filtrate fraction was spread out on the bottom of a small Petri dish for counting. The seston ash was later analyzed for phosphorus as indicated above.

The radioactivity determinations were made with a modified Scott type bell counter, filled with an argon-alcohol mixture at 10 cm. pressure, used in a thick lead shielding. This instrument gave a background count of 20 per minute, and permitted easy determination of the radioactivity of all the samples examined. All the radioactivity determinations are corrected for decay to correspond to August 8, the mid-point of the experiment. All have been corrected for variations in counter sensitivity to correspond to a sensitivity giving 150 counts per minute for an arbitrary uranium standard (2.53^{-3} g. Uranyl Acetate C. P.). The results given as counts per minute per cubic meter are set out in table III.

DISCUSSION OF THE RESULTS

Total recovery of radiophosphorus: It is immediately apparent from the table that significant amounts of radiophosphorus were recovered in all layers on all dates. The only way in which the radiophosphorus can be carried rapidly into the very stable hypolimnion of the lake is by the sedimentation of seston. The quantitative aspect of this process is of considerable interest. If the only movement occurring were vertical, the total quantity of radiophosphorus in the water under unit area of the deepest part of the lake, assuming a reasonably uniform original horizontal distribution, could not possibly be greater than the original introduction per unit area. Since the amount introduced corresponds to 1350×10^6 counts per minute, and the area of the lake is 94,400 m.^{2}, the upper limiting amount per square meter should be 14,300 counts per minute. The amount to be expected in a water column from 0–12.2 meters under unit area might be less than this, for the deepest layer studied is not quite the deepest layer of the lake and some radiophosphorus could have reached the bottom and could have been incorporated in the sediments. The actual values obtained by

TABLE III. *Quantities of radiophosphorus in Linsley Pond, by layers*

		August 1		August 8		August 15		August 22	
		Seston	Filtrate	Seston	Filtrate	Seston	Filtrate	Seston	Filtrate
I 0–1.75 meters	Counts per m.³ per min.	850	1600	770	1560	730	1250	750	2000
	Entire layer Millions counts per min.	128	241	116	235	110	188	113	301
II 1.75–3.5 meters	Counts per m.³ per min.	940	1410	730	1280	1020	1260	740	810
	Entire layer Millions counts per min.	117	176	91	160	128	157	93	101
III 3.5–5.3 meters	Counts per m.³ per min.	800	1490	1880	1080	1050	1620	1070	2040
	Entire layer Millions counts per min.	98	182	229	132	128	198	131	249
IV 5.3–7.0 meters	Counts per m.³ per min.	650	820	790	416	1100	1700	1210	1610
	Entire layer Millions counts per min.	64	81	78	45	109	168	120	159
V 7.0–8.8 meters	Counts per m.³ per min.	560	700	480	650	1060	150	630	1270
	Entire layer Millions counts per min.	36	45	31	42	68	10	40	81
VI 8.8–10.5 meters	Counts per m.³ per min.	550	420	260	390	1180	140	750	850
	Entire layer Millions counts per min.	22	17	10	16	47	6	30	34
VII 10.5–12.2 meters	Counts per m.³ per min.	420	510	860	460	—	710	710	1130
	Entire layer Millions counts per min.	10	12	21	11	(19)[1]	17	17	27
Sum, entire epilimnion (I, II) Millions of counts per min.		245 | 417 = 662		207 | 395 = 602		238 | 345 = 583		206 | 402 = 608	
Sum, entire hypolimnion (III–VII) Millions of counts per min.		230 | 337 = 567		369 | 246 = 615		371 | 399 = 770		338 | 550 = 888	
Sum, entire lake		1229		1217		1353		1496	
% Recovery in water		91.1		90.2		100.2		109.6	

[1] Sample lost: interpolated value used in sums.

summing from table III, and the percentage of the expected values are as follows:

Aug. 1	Aug. 8	Aug. 15	Aug. 22	
20,570	20,470	22,930	27,240	counts per min. per m.^{2}
144.3%	142.05%	160.4%	190.5%	

It will be observed that on every date the recovery, computed on the hypothesis of purely vertical movement of phosphorus, is impossibly high.

In table III the entries described as "entire layer, millions of counts per minute" refer to the product of the radioactivity per cubic meter and the volume of the layer. The sum of these products for any day (sum entire lake) gives the total amount of radiophosphorus actually in solution and suspension in the lake water. This quantity may then be compared with the amount of radioactive material introduced. It will be apparent that on the first two days about 90% of the material added is accounted for by this mode of calculation, while on the third day the radioactivity of the lake corresponds almost exactly to the added material. Only on the fourth day does an excess appear to have been present and, as is indicated below, this excess probably can be explained. These computations clearly indicate that when the sedimenting seston comes to rest on the mud at small and intermediate depths the radiophosphorus is rapidly liberated and passes out into the free water, being distributed in the same sort of way as is bicarbonate (Hutchinson, '41). Computation by entire layers is obviously the correct procedure and is employed in all further quantitative discussion.

Variation in the epilimnion: The total radiophosphorus in the top two layers is found to fall during the first three weeks of the experiment, but rises in the fourth week. The excess of radiophosphorus apparently present on August 22 is largely due to this rise, which concerns only the upper layer from 0 to 1.75 meters. The most reasonable explanation of the excess in this layer is that radiophosphorus previously held by marginal rooted vegetation was being rapidly liberated at this time and that an irregular distribution of radiophosphorus was set up, the water at the surface at the collecting station not being truly representative. It is reasonable to suppose that such a sudden liberation of phosphorus in the littoral as is implied was due to enhanced decomposition during the period of very high temperature that the surface layers had experienced. There is evidence that great superficial rises in total phosphorus may occur at the height of summer during Cyanophycean blooms (Hutchinson, '41; Einsele, '41) and are doubtless similarly determined by high superficial temperatures.

During the course of the period of the experiment the total phosphorus content of the entire epilimnion rose from 5.34 kg. to 6.66 kg. A least squares solution gives 0.32 kg. per week as the best value for the rate of increase, or 0.26 kg. per week for the period from August 1 to August 15. As it will appear from the next section, the hypolimnion was receiving at least 1.64 kg. phosphorus per week from the epilimnion during this period. It is evident therefore that the epilimnion was receiving 1.96 kg. of phosphorus per week from the littoral. Omitting the last week when a rise took place, the rate of decrease in radiophosphorus in the epilimnion, from August 1 to August 15, is about 40.10^6 counts per minute, while the hypolimnion is at the same time gaining radiophosphorus at the rate of about $101.5.10^6$ counts per minute. This implies that there must be a source of radiophosphorus other than the free water, from which the isotope can enter the epilimnion.

Samples of *Potamogeton crispus* from the north end of the lake were collected and their radioactivity and phosphorus contents determined; the results, given as counts per minute per gram and as % P, both referred to dry weight, and the specific activities as counts per minute per mg. P, are as follows:

Aug. 1	Aug. 8	Aug. 15	Aug. 22	
19.9	15.5	9.0	11.3	Counts per min. per gm.
0.216	—	0.285	0.190	% P.
9.2	—	3.2	5.9	Activity of P. Counts per min. per mg.

While the samples were small and may not have been representative of the lake as a whole, there is a clear indication of loss of radiophosphorus when the first two samples are compared with each other and with the third. In view of the slight increase on the last day, this decline may not be very significant.

At least between August 1 and August 15 radiophosphorus corresponding to 123 $\times 10^6$ counts per minute must have been liberated from the littoral plants or other marginal reservoirs to counterbalance the loss to the hypolimnion. If this radiophosphorus came from the plants, in which the specific activity is about 6.2 counts per minute per mg., it corresponds to 10 kg. per week. Since the known increment was only 1.96 kg. per week it is evident that either the plants contain mobile phosphorus of high and immobile phosphorus of low activity or that active phosphorus temporarily immobilized in the littoral sediments is involved. It is quite likely that the main littoral reservoir is in epiphytic diatoms and other algae with relatively short life-spans. If the amount liberated by the littoral be added to the total activity for the entire lake on August 1, it will become 1352 $\times 10^6$ counts per minute, or essentially the original sample put into the lake. Actually the analyses just given indicate that only about half the littoral supply was exhausted by August 15 or even by August 22, so that it is certain that any correction made to the August 1 figure, for the content of the marginal vegetation, will inevitably raise the total in the lake to an amount at least 10% in excess of the quantity introduced. There is evidently some error involved here, which is perhaps inherent in the morphometric data derived from Riley's ('39) map of the lake, or perhaps referable to some systematic instrumental error. In view of the fact that the experiment was not conducted under controlled laboratory conditions, but in nature, it is remarkable that such close agreement between the radioactive material introduced and that recovered can be obtained.

Variation in the hypolimnion as a whole: The total radiophosphorus content of the hypolimnetic layers III–VII is plotted against time in figure 2. It will be observed that the variation indicated by this plot possesses features of considerable interest. There is an initial rise of about 540 $\times 10^6$ counts per minute in the first week and then a slower and approximately linear rise throughout the second, third and fourth weeks of the experiment. The solid line fitted by least squares to the four points August 1, August 8, August 15, August 22 has a slope corresponding to 111.8 $\times 10^6$ counts per minute per week, so that the rate of increase during the first week was almost five times that in the subsequent weeks.

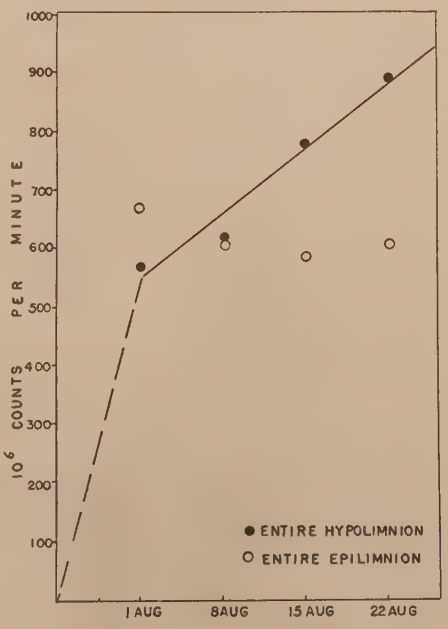

FIG. 2. Variation of the radiophosphorus contents of the epilimnion and hypolimnion.

The only reasonable explanation of these results is that initially the phytoplankton of the epilimnion took up the whole of the radiophosphorus, which, being introduced as phosphate, would be readily assimilable. At this time the sedimenting seston would presumably be much richer in P^{32} than at any later date. Later the phytoplankton may be supposed to have lost some of the phosphorus in a less assimilable, probably organic, form. Throughout the greater part of the experiment the distribution of radiophosphorus in the seston and in the free water may be regarded as representing an equilibrium between the seston, the less assimilable, and the ionic phosphate radiophosphorus. It is, therefore, obvious that only the radiochemical data of the period from August 1 to August 22 can be used in determining the rate of entry of phosphorus into the hypolimnion. The mean sestonic phosphorus content of the entire epilimnion during this period is 3.376 kg. while the mean P^{32} content of the same layer for the same date is 230×10^6 counts per minute. The rate of increase of radiophosphorus in the hypolimnion, namely 111.8×10^6 counts per minute per week, therefore, corresponds to a weekly passage of 1.64 kg. of sestonic phosphorus across the 3.5 meter plane in the middle of the thermocline. A similar computation, using only the data for the period August 1–August 15, gives a rate of increase of P^{32} of 101.5×10^6 counts per mm. per week corresponding to a weekly increment of 1.55 kg. phosphorus.

The total phosphorus of the hypolimnion increased throughout the period of the experiment until the last week. Unfortunately, two of the determinations at 10.5 meters given in table I are suspiciously low and almost certainly merely indicate incomplete reduction to the blue ceruleomolybdate used in the colorimetric determination of phosphorus. If, as seems probable, the 10.5 meter determination on August 22 is erroneous and if it be replaced by an interpolated figure, the hypolimnetic phosphorus rises, though less rapidly than before, throughout the last week of the experimental period.

If the period from August 1 to August 15 alone be considered, the total phosphorus of the hypolimnion rises at the rate of 3.75 kg. per week. During the same period it has just been shown that the rate of increase of radiophosphorus corresponds to a movement of 1.55 kg. of phosphorus per week from the epilimnion into the hypolimnion. It would appear, therefore, that during this period rather under half the increment in the hypolimnion is derived from the epilimnion and rather over half from some other source, that can only be mud in contact with the hypolimnetic water. If the corrected figure for the August 22 total phosphorus be acceptable, the least squares solution for the mean rate of increase of total hypolimnetic phosphorus is 3.1 kg. per week, while the rate of movement from the epilimnion is 1.64 kg. per week.

The dual origin of the phosphorus of the hypolimnion is in accordance with what is generally known about the phosphorus cycle in small lakes (Einsele, '36, '38; Hutchinson, '41). It is also apparent from an examination of the events in some of the individual layers, which provide evidence that the output of phosphorus from the sediments does not proceed uniformly at all hypolimnetic depths nor equally at all times during the period of the experiment.

The radiophosphorus content of layer III (3.5–5.3 m.): The radiophosphorus in this layer may be presumed to have entered the layer solely as sedimenting seston. The variability of the specific activity of the epilimnetic sestonic phosphorus is great enough to suggest rapid variations so that a mean value is probably best used in computing the quantity of phosphorus entering the hypolimnion. Using such a figure the amount of phosphorus in layer III that originated from falling seston can

	Aug. 1	Aug. 8	Aug. 15	Aug. 22
Computed	33.7 mg. per m.^{3}	43.7	39.2	45.8
Observed	31 mg. per m.^{3}	39	36	39

be computed and compared with the total phosphorus in the layer.

It will be observed that although the computed values are about 10% too high they vary with the observed values. The excess of the computed over the observed values suggests that the mean conversion factor used above may be a little too high. The general parallel variation of the observed and computed values, however, strongly supports the hypothesis that the whole of the phosphorus present at any time in this layer has been derived from seston falling from the layer immediately above it and that no phosphorus enters layer III from preexisting sediments in contact with the layer. On all occasions there is evidently a rapid liberation of soluble radiophosphorus from the falling seston. The radiophosphorus content of the sestonic phosphorus in the layer appears to fall progressively. Initially it is exactly 100 counts per minute per mg., falling to 55.3 counts per minute on August 15 and to 43 counts per minute on August 22. The mean value is 57.2 counts per minute per mg., which is little less than the mean epilimnetic value of 68.3 counts per minute per mg.

The radiophosphorus content of the lower layers of the hypolimnion: Throughout most of the hypolimnion there is an uncertainty as to how much of the seston phosphorus separated on the filter was really in suspension in the lake and how much was precipitated as ferric phosphate during filtration. This circumstance makes detailed quantitative treatment of the individual layers impossible, but a good deal can be learned from the specific activities of the total phosphorus at different depths on the various days on which samples were taken.

Reference to the total phosphorus contents of table II and the specific activities of table IV indicates quite clearly that the main rise in the total phosphorus of layer IV during the week August 1 to August 8 cannot have been due primarily to sedimenting plankton. The specific activity falls during a period of marked increase in total phosphorus content and it has already been indicated that during the period August 1 to August 15 the specific activity of the seston of layer III is considerably greater than that of layer IV either on August 1 or August 8. During the week of August 15 to August 22 the total phosphorus concentration remained practically unchanged in layer IV, the specific activity rose markedly, indicating a considerable replacement of the less radioactive phosphorus derived from the sediments by more radioactive phosphorus derived from falling seston.

The rise in total phosphorus in layer V during the week August 8 to August 15, though accompanied by a very slight rise in total radioactivity, leads to an overall decrease in specific activity, again indicating entry of phosphorus from the mud. As in layer IV, there is evidence of a

TABLE IV. *Specific activities of total and sestonic phosphorus counts per minute per mg.*

		Aug. 1		Aug. 8	Aug. 15		Aug. 22	
		tot.	sest.	tot.	tot.	sest.	tot.	sest.
I	0–1.75 meters	129	85	122	94	40.5	131	107
II	1.75–3.5 meters	107	94	86	91	42.5	55.5	57
III	3.5–5.3 meters	74	100	76	74	55.1	80	42.8
IV	5.3–7.0 meters	32	47.6	19.8	42.4	24.0	45.4	57.6
V	7.0–8.8 meters	14.6	15.1	12.8	10.2	13.6	16.4	15.4
VI	8.8–10.5 meters	6.7	11.0	5.0	12.2	17.6	—	9.0
VII	10.5–12.2 meters	4.4	2.8	5.5	—	—	—	6.1

replacement of some of this phosphorus by more radioactive phosphorus in falling seston during the last week of the experiment. While the events in the lowest two layers do not lend themselves to analysis, it is evident that in layers IV and V, but not in layer III, the dual origin of the phosphorus present is well established. It is probable that the mud surface in contact with layer III was still oxidized at the time of the experiment and that any phosphate that tended to leave the mud was precipitated in the oxidized microzone as $FePO_4$. The process of regeneration of phosphorus from falling seston at the mud surface is evidently a different process from that responsible for the rise of non-radioactive phosphorus in the deeper hypolimnetic layers.

Our best thanks are due to Miss Anne Carbone for much assistance in the determination of the radioactivity of our samples.

Summary

1. The movement of radiophosphorus added at the surface of Linsley Pond was studied over a four week period in summer.

2. Estimates of the total activities, corrected for decay, indicate that throughout this period phosphorus is sedimented from the epilimnion into the hypolimnion, but that such phosphorus as reaches the sediments is rather rapidly regenerated, passing again into the free water.

3. Phosphorus passes into the littoral vegetation and from such vegetation into the free water again. The specific activity of the phosphorus in material of *Potamogeton crispus* from the shallow water of the lake was always much less than that of the total epilimnetic phosphorus. It appears that an immobile fraction of low activity and a mobile fraction of high activity are present in the littoral zone. The mobile active fraction may be in part in epiphytic diatoms and similar short-lived organisms.

4. In the first week of the experiment the increment in activity in the hypolimnion below the 3.5 meter plane was five times as great as during the three subsequent weeks, during which it remained essentially constant. It is believed that immediately on addition practically the whole of the radiophosphorus enters the phytoplankton, which can easily be sedimented. During the first week phosphorus was probably lost from the phytoplankton in a form less easily assimilated than ionic phosphate. A steady state between ionic, less easily assimilable, and seston phosphorus is presumably set up.

5. There is evidence of movement of phosphorus into the hypolimnion both from the epilimnion and from the mud, but the latter process (other than regeneration at the mud surface) does not occur above 5.3 meters.

6. During the period August 1 to August 15, for which the best data are available, the following values for the rate of movement of phosphate in the lake were obtained.

Observed rate of increase in epilimnion	0.26 kg. per week
Loss to hypolimnion	1.55 kg. per week
Total movement from littoral into epilimnion	1.81 kg. per week
Observed rate of increase in hypolimnion	3.75 kg. per week
Gain from epilimnion	1.55 kg. per week
Gain from hypolimnetic sediments	2.20 kg. per week

Since the mean phosphorus content of the epilimnion is 5.82 kg. the observed rate of entry in this layer corresponds to replacement every three weeks. Since some phosphorus regeneration certainly occurs in the epilimnion the rate of plankton replacement must be somewhat greater.

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A QUANTITATIVE STUDY OF ATTACHMENT MATERIALS IN SODON LAKE, MICHIGAN

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INTRODUCTION

Knowledge of the productivity of water has been advanced through the study of a variety of indices of production. Clarke ('46: 323) enlarges on three basic concepts, namely (1) **standing crop**—the amount of organisms existing in the area at the time of observation; (2) **material removed**—the amount of organisms removed from the area per unit time by man, or in other ways; and (3) **production rate**—the amount of organisms formed within the area per unit time. The three ideas are closely related. Productivity measurements based on any one of the three are difficult to get and, once obtained, they are only partially satisfactory. Additional indices are needed even though they may be equally inadequate.

The exploratory work reported here finds its closest counterpart in production rate. The weight of attachment materials produced on a unit area of artificial surface (standard microscope slide) per unit of time has been measured. The attachment materials include organisms that attach and grow on the glass surface, and also any non-living particulate matter that becomes fastened directly to the glass or to the growth mat formed on the slide during the experiment.

That attachment materials offer one plausible basis for measuring water productivity was recognized as early as 1915 by Hentschel who measured the amount of materials growing on glass slides and on marine plants. Since that time several investigators have made use of the so-called "seeding-on" technic for several purposes (Willer, '20; Borner, '21; Naumann, '25; Thomasson, '25; Brehm and Ruttner, '26; Miller, '36; and Young, '45).

In 1947, a large-scale "seeding-on" experiment was initiated at Sodon Lake by the Cranbrook Institute of Science. Vertically arranged plastic slides attached to wooden blocks $6 \times 6 \times 6$ inches were used. It soon became obvious that the technic employed possessed several weaknesses that might be readily overcome. One question was whether the slide surface should be placed in a vertical or horizontal position. To answer this and related questions a series of comparative studies was undertaken by the writer in which standard microscope slides, 2.5×7.5 centimeters, placed in a horizontal position, and rectangular slides, 5.7×40.6 centimeters, suspended in a vertical plane, were employed. It was found that, during late summer and early fall, weights of organic matter (loss on ignition) from the vertical and horizontal surfaces were in the ratio of 1 to 6.6 (Newcombe, '49). In view of this finding the microscope slides that were used in the subsequent productivity studies reported upon here were suspended with their surfaces in a horizontal position.

Emphasis is given to the fact that the validity of "seeding-on" technics for measuring water productivity is by no means completely established. Some negative as well as positive properties of the method are indicated by this study and hence it is our purpose simply to set forth the methods employed, the results obtained and, too, certain desirable refinements in methodology suggested by the several experiments.

I am indebted to Emmy I. Hesz for assistance in making the organic matter determinations; to Dudley M. Blakeley

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for very useful suggestions regarding experimental surface materials; and especially to Dorothy M. Newcombe for valuable help in all phases of the field experiments.

Methods

The type of slide rack used was modeled after that described by Miller ('36: 126). Its dimensions are 45 × 10 × 2.5 centimeters and its wooden frame is grooved so as to hold 18 standard microscope slides (2.5 × 7.5 centimeters) in a horizontal position with surfaces facing upward and downward when the rack is suspended by a hook at the center of one end. Distance below the surface was measured to the center of the rack.

Three comparable collections for different types of analysis were obtained from each rack. One series was for surface scrapings (top and under surfaces were, with the exception of slides 9 and 10, kept separate) that were dried and ashed so as to provide a measure of the loss on ignition. A second series was mounted in glycerin for qualitative study of the material, while a third series provided surface scrapings for a chemical measurement of organic matter. The design of the experiment called for duplication of individual slide materials or groups of slides, for combining and separating the top and under surfaces of each slide or each group of slides, and for an eventual combining of the results obtained at opposite ends of the slide rack in order to yield an average that might reasonably be attributed to the depth represented by the level of the middle of the rack. These purposes were accomplished by means of the plan for collecting slide materials indicated below. The slides were numbered consecutively, starting at the end of the rack uppermost in the water. Except for the slight differences in level (the maximum distance is between slides 1 and 18, namely 37 centimeters), groups 1 and 1A are duplicates. T.S. = top surface; U.S. = under surface; and S.C. = surfaces combined.

Slide numbers of group 1	Types of slide collections	Slide numbers of group 1A
2, 5, 6	T.S. Loss by ignition	13, 14, 17
1, 5, 6	U.S. Loss by ignition	13, 14, 16
1, 3	T.S. Glycerin mount	16, 18
2, 4	U.S. Glycerin mount	15, 17
4, 7, 8	T.S. Organic matter	11, 12, 15
3, 7, 8	U.S. Organic matter	11, 12, 18
9	S.C. Loss by ignition	
10	S.C. Organic matter	

Various combinations of the data provided by this plan include a measure of the validity of either surface of one slide as compared with a corresponding surface of three or six slides for indicating the amount of organic matter produced per dm^2 area per 10-day period (Newcombe, '49). In most instances, the mean of the sum of the weights of groups 1 and 1A was taken to be the value corresponding to the subsurface level represented by the mid-point of the slide rack, i.e., halfway between slides numbered 9 and 10. Hence, practically all the mean weights presented here represent the mean of the weights of materials attached to six slides. Newcombe ('49) recommends that at least four slides be used particularly during periods of minimum growth.

The slide trays were suspended at different levels of station 1 located near the center of Sodon Lake and at 4 additional stations near shore under different environmental conditions of the littoral zone. While most of the slide racks suspended in Walnut Lake were lost, records covering the period September 20–November 25, 1947, were obtained at two littoral stations and serve as a basis of comparison with comparable environments in Sodon Lake. The results analyzed in this paper are confined to those that provide a measure of the amount of attachment material expressed in terms of total dry weight less the ash weight, thus giving the loss on ignition. As pointed out by Pennak ('45: 266) loss on ignition is a relative measure representing not only organic matter but volatile decomposition products from various salts.

Descriptive Remarks on the Stations Established in Sodon and Walnut Lakes

Sodon Lake, southeastern Michigan, is situated in Bloomfield Township, Section 20 at latitude 42°19′ and longitude 83°17′. A general description of the area and of the morphometric conditions of the lake is given by Newcombe and Slater ('49). Station 1 is situated near the center of the lake where the depth is about 17 meters. Here, slide racks were suspended at several levels. In most instances, those at 7.3 meters and below were lost due to the action of chemicals in the water on the untreated rope. Conditions at levels of 1.2 and 2.4 meters may be considered favorable for attachment of particulate or suspended matter (seston) throughout the period June 10 to November 23, 1947. At the 4.8 meter depth, however, the amount of dissolved oxygen during summer and early fall is extremely low and may be indirectly responsible for the relatively small amount of attachment that was observed.

Station 2 is at the dock where a slide rack was suspended at a depth of 1.2 meters (fig. 1). Due to activities on and around the dock conditions are regarded to be unnatural and this is reflected by the smaller percentage of organic matter (loss on ignition) in the attachment material.

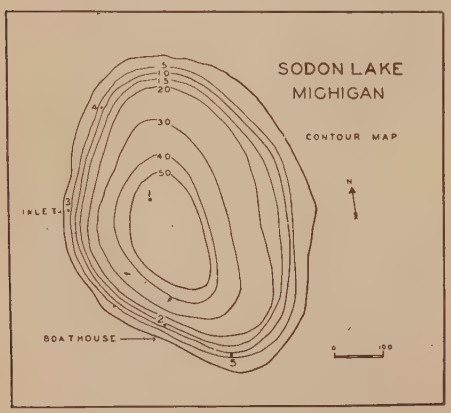

Fig. 1. A bathymetric chart of Sodon Lake showing the location of the stations. (*Original chart provided through the courtesy of the Institute for Fisheries Research, Ann Arbor, Michigan.*)

Station 3 is near the inlet and at a location where the depth of water is 0.6 meter. The slide rack was suspended with its uppermost part approximately at the water surface and this proved to be a most important factor determining the amount of attachment material. Water lilies are present within 0.6 meter of this station.

Station 4 occupies a littoral position north of station 3 and where the depth is about 2.4 meters. Here, the slide rack was suspended 1.2 meters below the surface. Nearby, there was a large amount of *Chara*.

Station 5 is also in the littoral zone but at the opposite end of the lake (fig. 1). The slide rack was placed at a level of 1.2 meters. Here, the depth of water is about 2.4 meters and the bottom of the rack was in close proximity to the *Chara* mat which explains the presence of numerous snails on the slides. These were removed prior to weighing. There are some water lilies 0.9 meter from the station.

Data are presented for two littoral stations situated on the west side of Walnut Lake in West Bloomfield Township, 1.5 miles southwest of Sodon. The area of Walnut Lake is 232 acres, its maximum depth being about 30.8 meters (Hankinson, '08). While Sodon is a small lake (area 5.7 acres) well protected from wind action, Walnut is relatively large and exposed to winds. Both stations are in a small cove where the littoral zone is dominated by a dense growth of *Chara*. The depth of water at station 1 is 2.4 meters and the slide rack was placed at a 0.6 meter level. At station 2 the water depth is about the same and the rack occupied a level of 0.6 meter below the surface. Due to a storm the level of this rack shifted somewhat but the main point of difference between the two slide racks at stations 1 and 2 appears to have been the proximity of the station 2 rack to *Chara*

during the period October 25 to November 25, 1947, resulting from the slight shift in position referred to above. Egg cases and Chironomid larvae were common on these slides. No other noticeable difference could be observed between the location of the two racks that might explain the significant and consistent differences in the quantity of attachment materials. For comparative data on the ecological conditions of these two lakes, the reader is referred to Hankinson ('08), Newcombe and Slater ('49, '50).

Results

The data obtained from this study show the extent of variation in the quantity of attachment material at different subsurface levels of Sodon Lake, at certain corresponding levels in different parts of the lake, and at corresponding levels and positions in Sodon and Walnut Lakes.

Sodon Lake

Station 1.—During the August–September period (33 days) by far the greatest amount of top surface attachment materials was obtained at depths of 1.2 and 2.4 meters, namely about 20 mgs per dm^2 area dry weight per 10-day period (table I). This represents the maximum amount in regard to both period and level. Figure 2 shows the amounts of top surface attachment materials at two levels for four periods from June 10 until November 23, 1947. A progressive increase is noticed at the 4.8 meter level whereas, at the 1.2 meter depth, lowest values were obtained during the two fall periods. It is interesting to find the percentage organic matter (loss on ignition) at the 4.8 meter level increasing from 34.1% during the August–September period to over 46% during the succeeding two periods or approximately equivalent to the percentage at the surface (table I). Data were not obtained for the loss on ignition in the case of the June–July–August samples (65-day period), the dry weights of which are given in figure 2. However, on a basis of other slide collec-

TABLE I. *Weights of attachment materials at three depths on the top and under surfaces of standard microscope slides during three comparable periods; weight is expressed in mgs per dm^2 area per 10-day period; O.M. = organic matter (loss on ignition, see text section on methods)*

Station 1

Depths in meters	Weights								
	Top surface of slide			Under surface of slide			Both surfaces combined		
	Dry	O.M.	%	Dry	O.M.	%	Dry	O.M.	%
Period of experiment: August 17–September 19, 1947: 33 days									
1.2	19.48	9.51	48.8	2.01	1.00	49.75	10.74	5.25	48.9
2.4	20.01	6.65	32.3	1.92*	0.93	48.4	12.42*	4.19	33.7
4.8	4.81	1.64	34.1	0.61*	0.37	60.7	3.44*	1.18	34.3
Period of experiment: September 21–October 24, 1947: 33 days									
1.2	8.72	4.32	49.5	2.38	1.89	79.4	5.55	3.10	55.8
2.4	6.98	3.98	57.0	2.07	1.77	85.5	4.52	2.87	63.5
4.8	8.84	4.28	48.4	0.80*	0.74	92.5	3.25*	2.04	49.9
Period of experiment: October 24–November 23, 1947: 30 days									
1.2	9.73	4.18	42.9	4.19	1.57	37.4	6.96	2.87	41.2
2.4	10.75	4.71	43.8	5.05	2.28	45.1	7.90	3.49	44.2
4.8	14.31	6.67	46.6	2.32*	0.48	20.68	7.92*	3.28	41.4

* One group only.

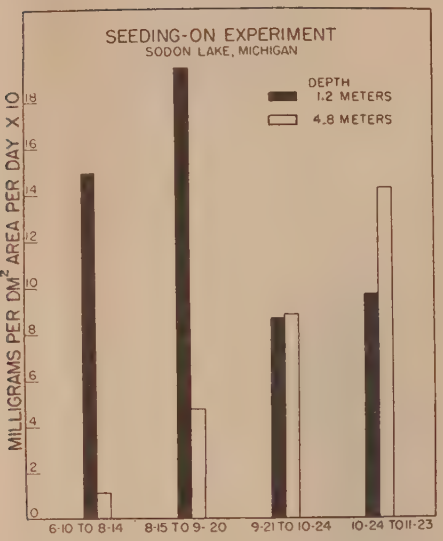

FIG. 2. Variations in dry weight of attachment material on standard microscope slides, at various levels and seasons.

tions during the first 41 days of this period, the percentage of loss on ignition at the 1.2 meter level was probably as high as 75. The only record for the 7.2 meter level was obtained during the period June 10–August 14, 1947, when the dry weight was 2.41 mgs per dm² area per 10-day period, over twice that for the 4.8 meter depth. The attachment material resembles a thin deposition of a calcium salt. A similar deposition accounts for the low percentage of organic matter at the 4.8 meter depth. While there may be some deposition at the 2.4 meter level that would lower the percentage of organic matter, this alone is not considered responsible for the low value of 32.3%. A relatively large amount of skeletal structure is noticeable on the duplicate slides mounted in glycerin and could account for the high ash weight, namely 13.3 mgs.

The quantitative relation between weight of attachment materials and depth is shown in figure 3 for the three periods of from 30 to 33 days in length. It is seen that in summer the amount of organic matter decreases toward the bottom, whereas, in the fall, an opposite trend is followed. Next to the largest amount of organic matter per dm² area per 10-day period, namely 6.67 mgs, was obtained during the late fall period and at the 4.8 meter level. It is surprising that no significant difference in percentage organic matter was represented. During the summer an abrupt decrease in the amount of periphyton on the suspension rope lines was clearly noticeable at the 3 meter level.

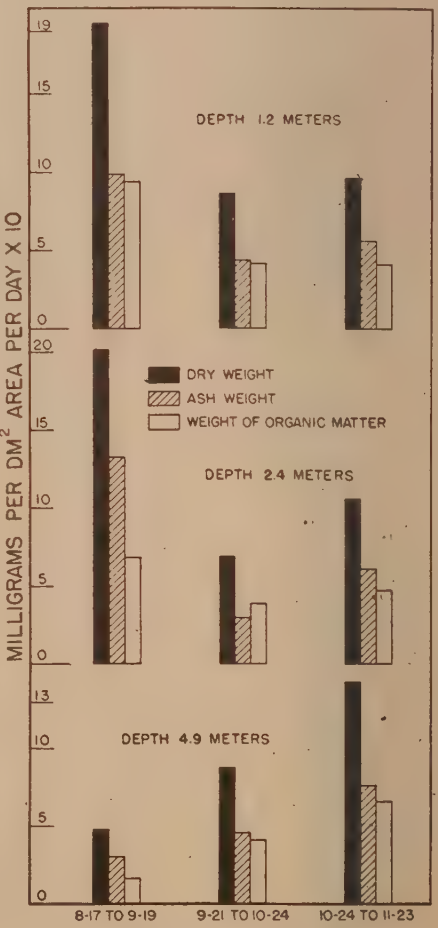

FIG. 3. Three weight measurements of the quantity of attachment materials on standard microscope slides kept at three levels in Sodon Lake throughout the period August 17 to November 23, 1947.

In general, the amount of attachment material on the under surface of slides submerged in these experiments was small and in some instances not enough to permit satisfactory measurements with a reasonable margin of error. However, this material provides the basis for several interesting implications. For example, the percentage organic matter at the 1.2 meter depth during the August–September period was about the same for both surfaces. One might expect a settling of inorganic particulate matter on the top surface that would lower the percentage of organic matter. During the September–October period the percentage organic matter on the under surface actually was a great deal higher than that of the top side, namely 79.4% at the 1.2 meter level.

Stations 2–5.—Table II gives a comparison of the amount of attachment material produced at five different stations. Contrary to expectation the quantity at stations 1 and 5 was quite similar, there being a somewhat higher percentage of organic matter at station 1. This is to be expected since more particulate inorganic substance is likely to exist in littoral waters.

Due to activity on the dock (station 2) inorganic particles settled on the top surfaces of the slides, thus accounting for the low percentage of organic matter, namely from 31 to 38%. The absolute weights of organic matter in the attachment material were likewise less than at comparable levels of other stations.

The heaviest weight of material was obtained at station 3 where the level of the slide rack was 0.23 meter. Here, the top surface dry weight was 27.50 mgs per dm^2 area per 10-day period. The percentage organic matter was normal in comparison with the majority of observations, namely 48.5%. While being near the inlet may have favored attachment and growth, it is likely that the high weights are due to proximity to the surface where there is more available light.

TABLE II. *Weights in mgs per dm^2 area per 10-day period of attachment material at five stations in Sodon Lake during three periods of similar length in 1947; standard-sized microscope slides were used; O.M. = organic matter (loss on ignition)*

Stations	Depth in meters	Exposure intervals	No. of days	Top surface of slide			Under surface of slide			Both surfaces combined			Av. % O.M. for top surfaces
				Weights			Weights			Weights			
				Dry	O.M.	%	Dry	O.M.	%	Dry	O.M.	%	
1	1.2	8/17– 9/19	33	19.48	9.51	48.8	2.01	1.00	49.75	10.74	5.25	48.9	47.07
		9/21–10/24	33	8.72	4.32	49.5	2.38	1.89	79.4	5.55	3.10	55.8	
		10/24–11/23	30	9.73	4.18	42.9	4.19	1.57	37.4	6.96	2.87	41.2	
2*	1.2	8/17– 9/21	35	11.60	4.40	34.5	1.70	1.53	90.0	6.65	2.97	44.7	34.7
		9/21–10/24	33	15.47	4.85	31.3	1.86	1.11	59.7	8.66	2.98	34.4	
		10/24–11/23	30	9.63	3.69	38.3	4.51	2.19	48.6	7.07	2.94	41.6	
3	0.23	8/17– 9/21	35	27.50	13.35	48.5	2.84	2.17	76.4	15.17	7.77	51.2	47.6
		9/21–10/24	33	17.02	7.77	45.6	3.35	2.33	69.5	10.19	5.02	49.3	
		10/24–11/23	30	12.60	6.15	48.8	4.88	1.95	40.0	8.74	4.09	46.8	
4	1.2	8/17– 9/21	35	9.72	4.78	49.2	1.54	1.49	96.7	5.63	3.14	55.8	47.5
		9/21–10/24	33	10.30	4.71	45.7	2.10	1.12	53.3	6.20	2.91	46.9	
		10/24–11/23	30	8.13	3.87	47.6	3.81	1.83	48.0	5.97	2.85	47.7	
5	1.2	8/17– 9/21	35	17.98	7.82	43.5	3.69	2.55	69.1	10.84	5.18	47.8	44.7
		9/21–10/24	33	6.08	2.86	47.0	1.86	1.06	57.0	3.97	1.96	49.4	
		10/24–11/23	30	10.07	4.40	43.6	4.10*	2.13	51.9	7.08	3.26	46.0	

* Means of three instead of six slides were used at this station.

TABLE III. *Weights in mgs per dm² area per 10-day period of attachment materials at two littoral stations in Walnut Lake during two periods of similar length in 1947. Standard-sized microscope slides were used; O.M. = organic matter (loss on ignition); depth = 0.6 meter*

Stations	Exposure intervals	No. of days	Top surface of slide			Under surface of slide			Both surfaces combined		
			Weights			Weights			Weights		
			Dry	O.M.	%	Dry	O.M.	%	Dry	O.M.	%
1	9/20–10/25	35	16.27	8.46	52.0	4.86	3.17	65.2	10.57	5.82	55.1
	10/25–11/25	31	67.32	17.40	25.8	8.69	4.24	48.8	38.00	10.82	28.5
2	9/20–10/25	35	28.95	15.65	54.1	7.49	5.22	69.7	18.22	10.44	57.3
	10/25–11/25	31	126.69	26.20	20.7	8.42	4.21	50.0	67.56	15.20	22.5

A conspicuous decrease in amount of attachment matter from summer to fall is clearly shown.

The slide rack at station 4 was at a 1.2 meter depth and the weights were unexpectedly low during the August–September period, being 4.73 mgs less in respect to organic matter than those of a corresponding level at station 1. In the fall there was a significant increase, the weights being comparable to those of stations 1 and 5. The average amount of organic matter for the two fall periods was 4.29 mgs per dm² area as compared with 4.25 mgs at the same level of station 1. It was expected that higher values would be obtained in inshore waters than at comparable levels near the center of the lake. The average per cent of organic matter in the top surface material for stations 1, 3 and 4 was found to be roughly 47, while that at station 5 was slightly less, namely 44.7%. The low weights at station 4 during the August–September period remain unexplained.

Walnut Lake

Stations 1 and 2.—Significantly higher weights of attachment material were obtained in the littoral zone of Walnut Lake (table III) than in corresponding locations and periods in Sodon. The level of the Walnut Lake slides was 0.6 meter; hence the results are not directly comparable to those from any single Sodon Lake experiment. However, the dry weights of station 1 for both seasons average much higher than those for station 3 in Sodon Lake despite the Sodon slides being at a depth of only 0.23 meter. We are unable to explain why consistently higher weights were obtained at station 2 than at station 1 in Walnut Lake. The low percentage of organic matter, namely from 20 to 25%, during the October–November period is probably due to the presence of larval insect tubes in the material.

A difference between the two periods is also seen in the amount of material on the under surface of the slides. Here, the amount is large enough to give reasonably accurate weighings. In both cases, lower percentages of organic matter were obtained during the late fall period, namely 48.8 and 50.0%. However, combining the results for both stations, the actual weight of organic matter for the late fall period was almost identical with that for the September–October period, namely 4.2 mgs per dm² area per 10-day period.

On account of the fact that the slide rack supports were not perfectly stationary, having been bent somewhat by fall storms, we cannot be sure of the factors which operated to produce the large differences between the slide collections at stations 1 and 2. The fact that the

one at station 2 was nearer to the *Chara* mat is considered to be partly responsible for the differences.

Discussion

Numerous investigators have submerged slides of different kinds in lake and stream waters for collecting animals and plants. Hentschel ('15) and Thomassen ('25) were among the first to suggest the use of "seeding-on" materials for indicating the productive capacity of water. Perhaps the majority of recent investigators depend on seston as the most reliable index of productivity. But, here, too, there are serious limitations. It is our belief that, while the obstacles to be overcome in using the attachment method are likely to be as great as those of other methods, nevertheless, it possesses merit and represents an additional index worthy of careful study.

It is necessary in the beginning to define the meaning of production rate for that is the ideal objective. Clarke ('46) defines it as the amount of organisms formed within an area per unit time. As he points out, the successive steps involved in such an analysis of production rate are numerous and interdependent. A slide is obviously a selective collector. We are not aware of any data showing the percentage of plankton forms in a particular body of water that do not attach to a designated surface such as glass, the one used in these experiments. ZoBell and Allen ('35) have used glass slides suspended in tandem for collecting bacteria from different levels. We have found that the green sulphur bacterium *Chlorobium limicola* Nadson readily "seeds-on" and it is likely that a considerable number of available forms readily become attached (Newcombe, '49). ZoBell refers to "attachment bacteria" whence our use of the term attachment materials when referring to the aggregate of organic and inorganic substance on the slide surface. Phytoplankters are abundant in the periphyton and seemingly represent the majority of the dominant algae, but on this there are no specific data. Protozoans may, on occasion, be extremely abundant in periphyton. On the other hand microcrustacea are not abundant. In the case of slides resting on or just above the *Chara* mat, the periphyton has been found to include Chironomid cases, amphipods, snails, egg masses, and microcrustaceans in considerable numbers. That large numbers of phytoplankters are represented in the periphyton is a distinctly positive consideration.

Our data have shown that in the littoral zone considerable inorganic detritus settles on the slides and for this a weight correction may be made. But difficulty lies in evaluating the effect of this detritus on subsequent attachment and growth. Varying amounts of partly broken down particulate matter that figure in the expression of organic matter are also present. It is likely that a satisfactory measure of this matter could be obtained experimentally.

Perhaps a major problem is that of differentiation between the amount of "seeding-on" and the increment of growth per unit of time. These processes go on concurrently. Production rate by definition refers to the amount of organisms formed within the area per unit of time. A small standing crop plus a high growth rate on the slides could theoretically yield the same amount of periphyton as a large standing crop and a slow rate of growth. It would seem desirable, therefore, to separate these components, although together they also possess some value. Doctor Donald E. Wohlshlag [2] has suggested (personal communication) that some degree of accuracy would be possible if the principle of "compound interest at a constant deposit rate" could be utilized. He calls attention to the following schedule based on the assumption that the amount of attachment materials, S, seeded-on each day does not grow during that day. The

[2] Department of Zoology, University of Wisconsin.

daily fractional increase is expressed by r. Thus,

Time	Total quantity on slide
At end of first day	S
At end of second day	$S(1 + r) + S = 2S + Sr$
At end of third day	$(2S + Sr)(1 + r) + S = 3S + 3Sr + Sr^2$
At end of fourth day	$(3S + 3Sr + Sr^2)(1 + r) + S = 4S + 6Sr + 4Sr^2 + Sr^3$

etc.

But, as Wohlschlag points out, "In actual practice, the true production rate would be rather difficult to determine even if the validity of the above assumptions was not questioned." The approach merits serious trial by experiment in an effort to appraise accurately the rates of change in the quantity of the several constituents that comprise the attachment material.

The results of this study indicate that under the conditions of the several experiments fairly satisfactory quantitative data may be obtained. It has been pointed out in a previous paper (Newcombe, '49) that a large enough slide should be used to yield an organic matter weight of at least 3 mgs and preferably 5 mgs. If a small slide is used the duration of the experiment must be correspondingly longer. Further, in certain places or during seasons of minimum attachment, a larger slide is considered desirable in order to help compensate for the small attachment and growth. It was also demonstrated that while three standard microscope slides give a fairly close approximation to six, one should probably use at least four slides.

Improvement over the technic employed in these experiments may be made by modifying the type of slide rack in the direction of simplification. A minimum of frame structure to which organisms may attach and grow should be the objective. Also, the design should expose to the slide surface as much as possible of the light available at the particular depth in question.

Regarding the composite weight data resulting from the 1947 measurements, it seems clear that the method is reasonably sensitive to differences in environment. Expectedly, the weights respond noticeably to changes in the amount of incident radiation. Much higher values were obtained at station 3, when the depth of the slides was only 0.23 meter, than at any of the deeper locations. It would seem that advantage of this fact might be taken to arrive at a closer measure of production rate. The amounts of dead and living organic matter settling on a slide surface at a 1 meter depth would presumably be less than that at a 2 meter depth, but in any case the difference is expected to be small. On the other hand, the amount of growth, i.e., production rate, would likely be much higher at the upper level due to light intensity, the dominant factor, being greater.

That the technic responds to differences in environmental factors is indicated by the seasonal trends in the weights of attachment material at the 4.8 meter depth of Sodon Lake (fig. 2). The magnitude of temperature variation with depth and the extent of the thermocline during the 1947 fall periods of the experiment are shown in figure 4. During the August–September and September–October periods there was no apparent surface temperature effect as far down as the 4.8 meter level. Any effect of the surface mixing during these two periods would be indirect. The progressive increases at this level, shown in figure 2, strongly suggest that such indirect effects were indeed a reality. The maximum increase in weight took place during the late-fall period. Apart from the lower temperature condition of this period, a higher growth is expected because studies of Newcombe and Slater ('50) show that the levels of higher nutrients as well as

of higher concentrations of dissolved oxygen were much deeper than during the two preceding periods. During summer and early fall the oxygen content at depths of around 5 meters was found to be extremely low, a condition less favorable for high periphyton production.

Comparison of the weights at the littoral stations in Sodon and Walnut Lakes show a much higher production in the waters of the latter lake. This corresponds with the conclusions of Newcombe and Slater ('50), based on nannoplankton organic matter measurements. Littoral measurements offer technical difficulties. Here, there is likely to be considerable dislodged periphyton in the plankton drift and, too, local concentrations of littoral fauna may be expected to produce irregularities in the results.

Young ('45) was able to point out important differences between periphyton on non-living and that on living substrata. For example, he failed to find any *Gloeotrichia* on rope or on glass slides placed within a clump of bullrushes bearing the blue green alga. This opens up another aspect of the "seeding-on" technic in need of elaboration.

Summary

This paper embodies the results of 10 slide rack experiments conducted in Sodon and Walnut Lakes, southeastern Michigan during the period June 10–November 23, 1947.

The maximum weight of attachment material obtained at the 1.2 meter level in Sodon Lake was approximately 20 mgs per dm² area per 10-day period during the interval from August 17 until September 19, 1947. There was a pronounced decline to about 9 mgs for each of the two succeeding fall periods ending November 23.

A progressive increase in weight of attachment material at the 4.8 meter level was observed from the period June 10–August 14 when the weight was 1.15 mgs to the interval October 24–November 23

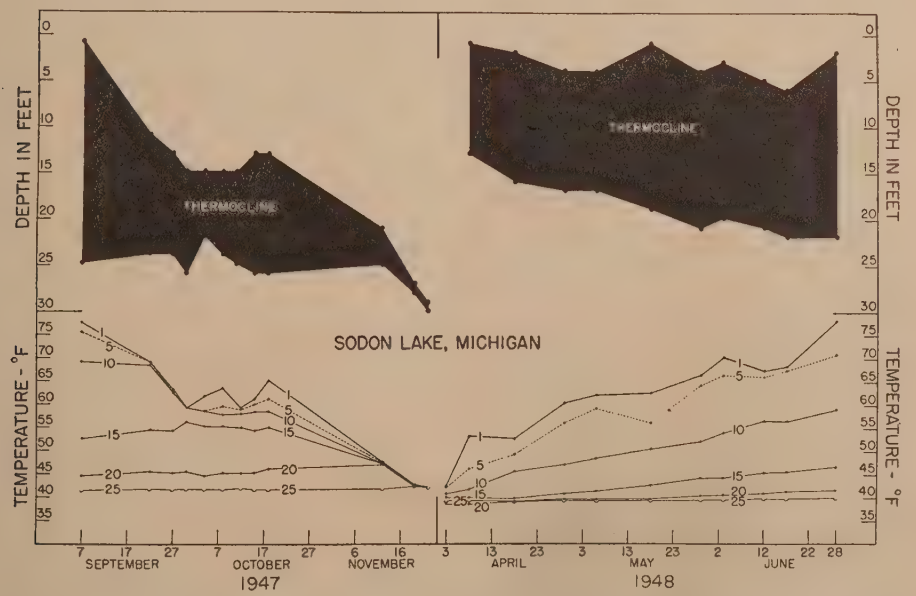

Fig. 4. Subsurface temperatures and the extent of the thermocline during the concluding periods of the 1947 experiments referred to in figures 2 and 3 (*after Newcombe and Slater, '49*).

at which time the weight amounted to 14.31 mgs per dm^2 area per 10-day period. This trend is attributed in large part to an increase in the productivity of a gradually deepening surface stratum of water brought about by lower fall temperatures.

A small difference in depth of the attachment surface is a dominant factor in determining the weight of slide material. By employing this relation, it seems likely that a useful expression of actual production rate may be developed.

During summer the productive stratum of Sodon Lake extends to a depth of about 3 meters. This level is suggested by the vertical experiments and by the conspicuous zonation on rope supports.

Unexpectedly, no significant difference was observed between the weights obtained at station 1 in the center of the lake and those at station 5 in the littoral zone, depth 1.2 meters. Here, the percentage organic matter ranged from 43 to 50, for the top slide-surface materials. Usually, higher percentages were found for the under slide-surface, due in large part to lack of exposure to descending inorganic particulate matter and also because of the greater margin of experimental error resulting from the smaller amount of material present.

The weight data for Walnut Lake confirm our previous conclusion based on nannoplankton organic matter measurements, namely, that the waters of this lake are more productive than those of Sodon.

In Walnut Lake, consistent differences in the per cent of organic matter in the attachment materials were observed. During the period September 20–October 25, the top-surface material averaged approximately 53% in comparison with a corresponding average of 67% for the under-surface substance.

The maximum amount of material obtained in any experiment was a dry weight of 126.69 mgs per dm^2 area per 10-day period of which 20.7% was organic matter. This experiment was conducted at a 0.6 meter level in the littoral zone of Walnut Lake during the period October 25–November 25, 1947. The exceptionally high value is attributed to the proximity of the slide rack to the *Chara* mat resulting in the presence of numbers of Chironomid larvae, egg cases and additional smaller animal materials on the slides.

A presentation of certain points bearing on the validity of attachment material for indicating water productivity is given. Also, suggested means for improving and standardizing a suitable "seeding-on" technic are treated briefly.

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FOOD RELATIONSHIPS OF THE MINNOWS OF THE DES MOINES RIVER, IOWA [1]

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INTRODUCTION

Food may be an important factor affecting the abundance of fish in a body of water. The present paper, part of more extensive ecological study, is concerned with the seasonal variations in the food consumed by several species of minnows in a section of the Des Moines River. The distribution and abundance of the minnows and other fishes known to occur in this section of the River and in other Boone County streams has already been presented (Starrett, '50). The changes in abundance of the various species of minnows and some of the factors causing these changes will be discussed in a later paper.

RESEARCH AREA

The Des Moines River is the largest river flowing through Iowa. It arises in a glacial moraine in southwestern Minnesota and flows in a southeasterly direction across Iowa to the Mississippi River. The Des Moines is 535 miles in length and has a total drainage area of 14,500 square miles of which 93 per cent is devoted to farming (U. S. 71st Congress Report).

About midway in its course, it passes through Boone County, cutting a deep valley in the otherwise flat land (figure 1). At one point in Boone County, 257.8 miles above the mouth of the river, the total drainage is 5,610 square miles. The stream gradient is 1.5 feet per mile for the lower 300 miles of the river which includes Boone County. The next 80 miles have a steeper slope of 3.2 feet per mile, and in the upper part of the river the gradient is 2.2 feet per mile (U. S. 71st Congress Report).

The average annual rainfall for the entire Des Moines River watershed is 30.07 inches (U. S. 71st Congress Report) and for Boone County the average is 31.67 inches (U. S. Dept. of Agric. Rept. 1941). The heaviest precipitation of the year usually occurs in May and June, causing high water stages in the river. Frequently an early spring flood follows thawing and fast run off of the water. Cloudbursts and heavy rains occasionally cause local temporary floods in summer and floods are not uncommon in early fall.

The turbidity of the water increases with a rising river. Secchi disc readings of 10 cm. and 10.4 cm. were recorded during periods of high water. During high water the turbidity is largely caused by silt. The turbidity in periods of low water during the summer varies with the production of *Microcystis aeruginosa* Kütz. In the summer of 1946 Secchi disc readings ranged from 16.5 cm. to 35 cm.; whereas, by the middle of October of that year, *Microcystis* was greatly reduced in numbers and a Secchi disc reading of 86.75 cm. was recorded. Usually

[1] Iowa Cooperative Fishery Research Unit. Project No. 36, sponsored by the Industrial Science Research Institute of Iowa State College and the Iowa State Conservation Commission. Part of a thesis submitted to the Graduate Faculty of Iowa State College as partial fulfillment of requirements for the degree of Doctor of Philosophy.

[2] The writer wishes to express his appreciation to Drs. Kenneth D. Carlander and George O. Hendrickson of Iowa State College under whose guidance this investigation was made. Acknowledgment for aid in identification of certain food items is due Dr. Elmo Hardy and Dr. H. H. Knight, of Iowa State College; Dr. A. C. Martin, of the U. S. Fish and Wildlife Service; and Mr. A. R. Brooks, of the Department of Agriculture of Canada. The writer wishes to thank Mr. Don Briden and others for assistance in the field.

[3] Now Associate Aquatic Biologist with the Illinois Natural History Survey, Urbana, Illinois.

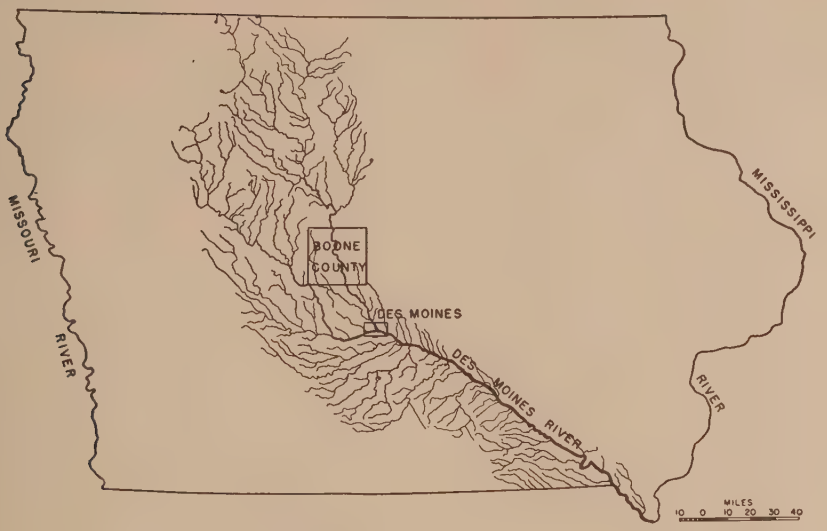

FIG. 1. Des Moines River Watershed showing the Boone County study area.

the river is covered with ice from late December through the middle of March. During this period the water is clear.

No large streams empty into the river in Boone County, and the runoff is carried by a number of small temporary and a few permanent creeks. The hillsides of the valley are partially to fully timbered (oak-hickory) and are partially grazed. Suitable land in the valley is under cultivation. The banks bordering the river have a sparse to thick growth of willow, cottonwoods, boxelder, American elm, and soft maple. The higher aquatic plants are absent from the river, probably because of the current, constant fluctuations of water level, and turbidity.

The bottom of the river is chiefly sand-gravel, with sand-silt, rubble and boulders in limited areas. At low water levels many sand, gravel and rubble bars appear and the remaining shoreline has steep cut banks with an occasional rock outcrop. The channel at low water stages varies in depth from 1.5 to 4 feet. Deep holes are present below bars and at bends. The river has few connecting sloughs and backwaters, except during high water, and adjoining bottomland lakes are conspicuously absent.

Silt was the only type of pollution observed during the course of this investigation. In some years winter kills of fish have been noted by local residents.

A section of the Des Moines River (Yell Twp., Sec. 2: Station 2) below the Fraser dam was selected for the principal studies because of accessibility for seining operations. The slope and locations of the bluff permitted seining during periods of high water. Below the dam part of the channel remained open through the winter months permitting the collection of minnows for food habit studies. Sand and sand-gravel were the principal type of bottom at this station. This station is approximately the half-way point on the river, 262.2 miles from the source and 262.8 miles from the mouth (figs. 1 and 2).

Collections were also made at two other stations. Station 1 (Pilot Mound Twp., Sec. 27) was established 2 miles above the lowhead dam at Fraser. The current was slower here than at the other two stations and the bottom was mostly sand-silt. Station 3 (Marcy Twp., Sec. 18) was near the town of Moingoina, 16.8 miles below Station 2. More rubble

bottom is present in this locality than at other stations.

The other stations on the river were used only temporarily and were located between stations 2 and 3. The bottom and current at these stations were similar to those given for stations 2 and 3.

General

Competition for food may occur not only between individuals of the same species but also between fish of different species. A very abundant species in the presence of a limited food supply would be confronted only with intraspecific competition; however, a large population of mixed species encountering the same condition would be involved with inter- and intraspecific competition. Forbes ('14, pp. 3–4) states that:

> "fishes have a common body of food resources of miscellaneous character upon which many of them draw almost indiscriminately according to circumstances at the time, but that from this common mass of resources, habits, and capacities there is a tendency to specialize in various directions, which tendency goes to its limit in some species, halts at various intermediate stages in others, and in still others is hardly discernible at all."

The various species in the Des Moines River have followed the pattern described by Forbes. Some have a specialized diet, others are partially specialized, whereas the southwestern sand shiner is quite omnivorous. The specialized feeders have little change in type of food through the various seasons. In the Des Moines River these specialized feeders may be classified into two groups. One type feeds on bottom ooze, and the other on

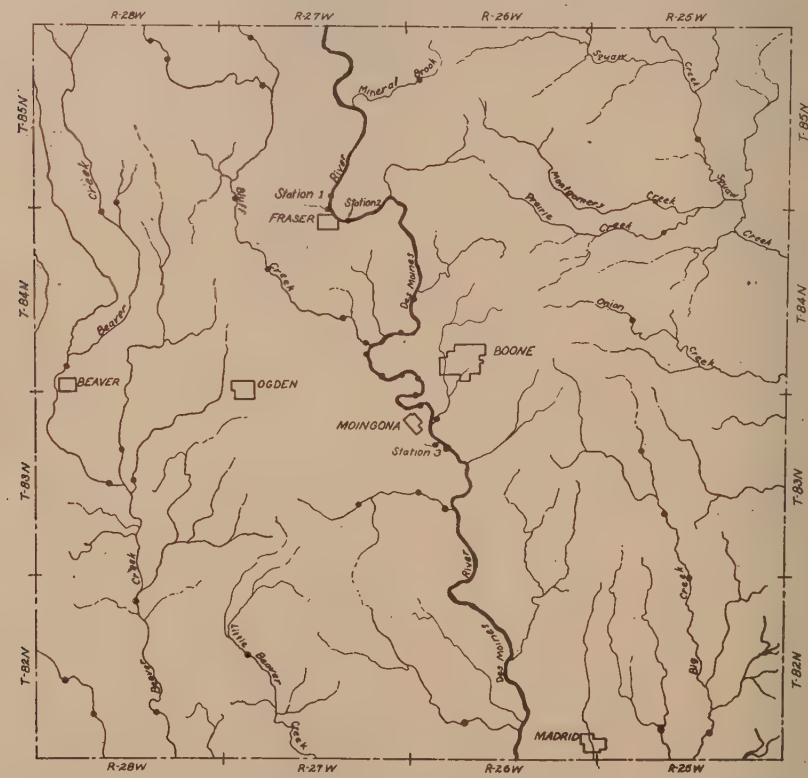

Fig. 2. Points at which fish collections were taken in Boone County, Iowa (1946–48).

dipterous larvae. The diets of the other minnows are modified by seasonal changes and availability of foods. Several species tend to select certain foods from a variety of abundant foods.

The food habits of thirteen species of minnows were studied, and a few observations were also made on seven less abundant species. The total of 3,033 minnows examined included the following species:

Northern creek chub—*Semotilus atromaculatus atromaculatus* (Mitchill)
Hornyhead chub—*Nocomis biguttatus* (Kirtland)
Silver chub—*Hybopsis storerianus* (Kirtland)
Speckled dace—*Extrarius aestivalis* (Girard)
Western blacknose dace—*Rhinichthys atratulus meleagris* Agassiz
Western golden shiner—*Notemigonus crysoleucas auratus* (Rafinesque)
Common emerald shiner—*Notropis atherinoides atherinoides* Rafinesque
Rosyface shiner—*Notropis rubellus* (Agassiz)
Northern common shiner—*Notropis cornutus frontalis* (Agassiz)
Spotfin shiner—*Notropis spilopterus* (Cope)
River shiner—*Notropis blennius* (Girard)
Central bigmouth shiner—*Notropis dorsalis dorsalis* (Agassiz)
Southwestern sand shiner—*Notropis deliciosus deliciosus* (Girard)
Suckermouth minnow—*Phenacobius mirabilis* (Girard)
Brassy minnow—*Hybognathus hankinsoni* Hubbs
Fathead minnow—*Pimephales promelas promelas* (Rafinesque)
Bullhead minnow—*Ceratichthys perspicuus* (Girard)
Bluntnose minnow—*Hyborhynchus notatus* (Rafinesque)
Central stoneroller—*Campostoma anomalum pullum* (Agassiz)

Afield the specimens designated for use in food studies were suffocated prior to preservation in formalin (Webster, '43). In the laboratory the entire digestive tract was examined for food items. An estimate of the volume of each food item was made and recorded as percentage of estimated total volume of the digestive tract. If an item occurred only as a trace, it was recorded as 1 per cent. With the four species of Des Moines River minnows possessing long, coiled intestines, the contents of the digestive tract were examined at intervals along the tract (Kraatz, '23).

Minnows used in the food study were collected from the Des Moines River during each month between April 9, 1946, and July 10, 1947. During the course of each week in the summer and fall of 1946, collections were taken so as to cover each 4-hour period day and night. From these data the feeding trends of the minnows could be determined. These data were grouped into the following seasons or periods for comparative purposes:

Spring 1946—April 9 through June 17
High water 1946—June 18 through June 26
Summer 1946—June 27 through September 18
Fall 1946—September 19 through November 23
Winter 1946–47—November 24 through March 31
Spring 1947—April 1 through June 1
High water 1947—June 7 through July 10

This paper does not include the detailed food habit studies made of the various species of minnows in this investigation, but is instead a compilation of the food habits into broad classifications to determine food relationships among the minnows.

Feeding Trends

Seining and trapping operations in the Des Moines River indicated that three abundant species of minnows (spotfin shiner, southwestern sand shiner, and bullhead minnow) are active during the daylight hours and are relatively inactive at night (Starrett, '50). The estimated volume of food in the digestive tracts of these species decreases during the night,

indicating little or no feeding after dark. The volumetric determinations of food items in the spotfin shiner, based on 457 specimens taken at various times of day and night during the summer of 1946, indicate an increase in feeding through the day, reaching a maximum by late afternoon and dusk (table I). The decrease in volume in the night collections indicates that this species does little feeding at night. The volumetric data for the other species of minnows indicate a similar trend. The fall data are also indicative that the river minnows are mainly diurnal feeders. The activity of the minnows determined by trappings and seining seems to correspond with the diurnal feeding trend.

Bajkov ('35) mentions that our knowledge regarding the daily consumption of fish under natural conditions still is very meager. Although no attempt was made in this study to determine the exact food consumption, the data do indicate that the minnows feed daily and that the rate of digestion is quite rapid during the warmer months. Ricker ('46) summarizes the literature on the rate of feeding of fishes in relation to temperature and states that for the few species of fishes that have been studied there appeared to be an optimal range correlated with summer temperatures in the natural habitat. The total volume of food in the various species of minnows was lowest in winter and spring. The water temperatures in the winter of 1946–47 at station 2 ranged from 32° to 35° F. The lower temperatures were accompanied by a reduction in available fish foods. In the winter there is a complete absence of terrestrial insects and emerging aquatic insects in the Des Moines River. These insects did not appear in the minnows' diet until late April and early May.

High-water stages also affect the availability of food. The quantity of food is reduced for bottom feeding minnows more than for the surface feeders. During the periods of high water, the bottom microflora is scoured, and the bottom ooze feeders examined from high-water collections contained mud and few diatoms. The availability of insect larvae to minnows is probably limited by the increased turbidity and volume of water. Fishes able to adapt themselves to surface feeding were found to take terrestrial invertebrates and plant materials during high-water stages.

On the Des Moines River the emergence of Ephemeroptera and Trichoptera seemed to be mainly in the late afternoon and dusk hours. An increase of these insects was noted in the food of certain minnows collected at dusk. Emerging Diptera were found in the digestive tracts throughout the day. The emergence of the subimago stage of Ephemeroptera, according to Needham, Traver, and Hsu ('35), appears to be at different periods of the day for various species.

No noticeable differences were found in the feeding habits of minnows collected at the three principal stations established on the river. These data are therefore combined rather than listed by individual station.

TABLE I. *Average volume of food in spotfin shiner* (Notropis spilopterus) *at various periods throughout day and night, Des Moines River, Summer, 1946*

Time*	0800–1000	1000–1400	1400–1700	2000	0000	0400
No. collections	19	16	14	10	9	10
No. specimens	90	77	88	56	77	69
Percentage empty	9	8	2	11	32	67
Average volume of food as percentage of digestive tract volume	13	17	19	26	14	2

* Time is recorded on the 24 hour basis. Midnight is 0000 and 10:00 P.M. is 2200.

TABLE II. *Comparison of food habits of the more abundant species of minnows, Des Moines River (Summer)**

Species of Minnow (Cyprinidae)	Percentage of fish containing item and (in parenthesis) percentage of total volume											Summary			
	Bottom ooze	Plant material	Adult terrestrial insects	Adult and emerging Diptera	Corixidae	Ephemeroptera nymphs**	Trichoptera larvae**	Dipterous larvae**	Aquatic nymphs and larvae**	Adult and emerging Ephemeroptera	Miscellaneous	No. fish examined	No. fish empty	No. collections	Avg. volume of food as percentage of digestive tract volume
Omnivorous															
N. deliciosus	50(68)	11(2)	9(3)	11(1)	1(1)	22(11)	9(5)	8(1)	37(22)	2(2)	(2)	153	8	44	40
Semi-Specialized															
N. spilopterus	5(3)	24(24)	23(18)	35(7)	1(1)	20(14)	9(16)	18(1)	43(36)	5(6)	(6)	311	22	59	18
N. dorsalis	24(31)	6(2)	10(5)	14(4)	2(1)	16(21)	8(8)	40(1)	58(52)	1(1)	(6)	122	12	34	19
N. cornutus	24(14)	34(20)	26(18)	17(3)	0(0)	41(30)	4(10)	0(0)	46(42)	1(1)	(3)	76	2	36	27
S. atromaculatus	0(0)	8(2)	17(38)	17(7)	0(0)	17(22)	8(2)	8(1)	41(36)	0(0)	(17)	12	5	12	8
N. rubellus	15(15)	5(1)	15(15)	40(15)	5(3)	10(10)	0(0)	20(1)	25(13)	20(28)	(10)	20	2	10	10
C. perspicuus	17(41)	0(0)	0(0)	17(5)	0(0)	8(5)	8(20)	8(1)	42(49)	0(0)	(5)	12	1	7	8
Diptera Feeders															
E. aestivalis	0(0)	0(0)	0(0)	22(5)	0(0)	19(58)	6(3)	59(1)	72(87)	0(0)	(8)	68	8	17	8
P. mirabilis	16(6)	0(0)	0(0)	16(13)	0(0)	4(11)	12(18)	82(1)	68(76)	0(0)	(5)	25	5	15	9
Bottom Ooze Feeders															
H. notatus	80(94)	0(0)	0(0)	0(0)	0(0)	7(6)	0(0)	0(0)	7(6)	0(0)	(0)	15	2	10	58
H. hankinsoni	100(100)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	11	0	9	65
C. anomalum	100(100)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	4	0	4	80
P. promelas	100(100)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	6	0	5	68

* Period from June 27 through September 18, 1946. Collections taken between 0800 and 2100. Water temperatures ranged from 72° F. to 85° F.; and water levels from 0.33 feet to 2.96 feet.

** Columns under heading "Aquatic nymphs and larvae" include Ephemeroptera nymphs, Trichoptera and Diptera larvae, as well as Coleoptera, Hemiptera, and others.

TABLE III. *Comparison of food habits of the more abundant species of minnows, Des Moines River (Fall)**

Species of Minnow (Cyprinidae)	Percentage of fish containing item and (in parenthesis) percentage of total volume											Summary			
	Bottom ooze	Plant material	Adult terrestrial insects	Adult and emerging Diptera	Corixidae	Ephemeroptera nymphs**	Trichoptera larvae**	Dipterous larvae **	Aquatic nymphs and larvae**	Fish	Miscellaneous	No. fish examined	No. fish empty	No. collections	Avg. volume of food as percentage of digestive tract volume
Omnivorous															
N. deliciosus	90(94)	8(1)	5(1)	8(1)	5(1)	1(1)	1(1)	8(1)	10(2)	0(0)	(0)	77	2	25	38
Semi-Specialized															
N. spilopterus	6(7)	25(5)	34(49)	41(16)	9(5)	4(2)	1(1)	8(1)	20(10)	0(0)	(8)	106	26	25	10
N. dorsalis	41(45)	11(2)	23(14)	39(16)	4(8)	7(4)	3(3)	13(1)	20(11)	0(0)	(4)	70	6	21	11
N. cornutus	48(34)	38(7)	34(35)	13(2)	17(6)	15(4)	6(2)	2(1)	25(6)	13(6)	(4)	48	0	21	31
S. atromaculatus	5(2)	5(5)	11(2)	5(1)	16(19)	5(1)	0(0)	0(0)	5(1)	53(70)	(1)	19	5	12	15
N. rubellus	6(3)	0(0)	53(69)	44(12)	3(2)	9(3)	0(0)	6(1)	15(7)	0(0)	(7)	34	6	13	14
C. perspicuus	34(20)	49(69)	4(2)	13(2)	4(2)	0(0)	4(1)	4(1)	9(2)	0(0)	(3)	53	6	14	23
Diptera Feeders															
E. aestivalis	1(1)	0(0)	1(3)	9(6)	0(0)	0(0)	7(46)	47(1)	59(76)	0(0)	(15)	85	27	23	7
P. mirabilis	17(11)	0(0)	0(0)	14(2)	3(1)	0(0)	19(37)	78(1)	86(81)	0(0)	(5)	36	3	14	11
Bottom Ooze Feeders															
H. notatus	100(100)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	6	0	5	36
H. hankinsoni	100(100)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	5	0	4	28
C. anomalum	100(100)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	2	0	2	58
P. promelas	100(100)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	2	0	2	58

* Period from September 19 through November 23, 1946. Collections were taken between 0800 and 2000. Water temperatures ranged from 34° F. to 65° F.; and water levels from 0.48 feet to 1.20 feet.

** Columns under heading "Aquatic nymphs and larvae" include Ephemeroptera nymphs, Trichoptera and Diptera larvae as well as Coleoptera, Hemiptera, and others.

TABLE IV. *Comparison of food habits of the more abundant species of minnows, Des Moines River (Winter)**

Species of Minnow (Cyprinidae)	Percentage of fish containing item and (in parenthesis) percentage of total volume										Summary			
	Bottom ooze	Plant material	Corixidae	Ephemeroptera nymphs**	Trichoptera nymphs**	Dipterous larvae**	Aquatic nymphs and larvae**	Fish	Entomostraca	Miscellaneous	No. fish examined	No. fish empty	No. collections	Avg. volume of food as percentage digestive tive tract volume
Omnivorous														
N. deliciosus	41(65)	0(0)	0(0)	3(2)	6(10)	47(1)	48(33)	0(0)	19(2)	(0)	73	8	16	11
Semi-Specialized														
N. spilopterus	0(0)	2(1)	4(27)	2(8)	6(6)	43(1)	49(65)	0(0)	16(6)	(1)	49	18	18	3
N. dorsalis	2(1)	0(0)	2(1)	5(5)	14(25)	68(1)	88(92)	0(0)	40(6)	(0)	57	15	15	6
N. cornutus	8(3)	4(1)	12(22)	20(50)	16(6)	40(1)	60(65)	4(7)	24(3)	(0)	25	2	9	17
S. atromaculatus	0(0)	0(0)	11(19)	22(26)	33(6)	22(1)	67(49)	11(31)	11(1)	(0)	9	1	8	18
N. rubellus	0(0)	0(0)	0(0)	14(9)	0(0)	43(1)	42(100)	0(0)	0(0)	(0)	7	4	4	2
C. perspicuus	0(0)	5(14)	10(3)	0(0)	10(8)	60(1)	70(74)	0(0)	25(4)	(5)	20	3	6	7
Diptera Feeders														
E. aestivalis	0(0)	0(0)	0(0)	0(0)	3(16)	84(1)	84(98)	0(0)	5(2)	(0)	38	6	14	3
P. mirabilis	0(0)	0(0)	0(0)	0(0)	3(1)	94(1)	94(98)	0(0)	0(0)	(2)	33	2	13	5
Bottom Ooze Feeders														
H. notatus	50(87)	0(0)	0(0)	0(0)	0(0)	17(1)	33(13)	0(0)	0(0)	(0)	6	1	6	17
H. hankinsoni	75(100)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	8	2	8	5
C. anomalum	100(99)	0(0)	0(0)	0(0)	0(0)	25(1)	25(1)	0(0)	0(0)	(0)	4	0	4	37
P. promelas	100(100)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	1	0	1	1

* Period from November 24, 1946 through March 31, 1947. Collections taken between 0800 and 1630. Water temperatures ranged from 32° F. to 42° F.; and water levels from 0.40 feet to 3.00 feet.

** Columns under heading "Aquatic nymphs and larvae" include Ephemeroptera nymphs, Trichoptera and Diptera larvae, as well as Coleoptera, Hemiptera, and others.

TABLE V. *Comparison of food habits of the more abundant species of minnows, Des Moines River (Spring)**

Species of Minnow (Cyprinidae)	Percentage of fish containing item and (in parenthesis) percentage of total volume												Summary			
	Bottom ooze	Plant material	Adult terrestrial insects	Adult and emerging Diptera	Corixidae	Ephemeroptera nymphs **	Trichoptera larvae**	Dipterous larvae **	Aquatic nymphs and larvae**	Fish	Lepidopterous larvae*	Miscellaneous	No. fish examined	No. fish empty	No. collections	Avg. volume of food as percentage of digestive tract volume
Omnivorous																
N. deliciosus	16(59)	33(7)	2(1)	16(3)	4(2)	16(10)	11(8)	18(1)	36(23)	0(0)	7(5)	(1)	45	3	17	15
Semi-Specialized																
N. spilopterus	0(0)	20(6)	9(11)	36(18)	2(4)	16(9)	0(0)	11(1)	22(13)	0(0)	9(26)	(22)	45	8	16	3
N. dorsalis	0(0)	21(7)	8(5)	8(4)	4(7)	8(11)	7(4)	38(1)	51(41)	0(0)	6(33)	(3)	53	8	19	6
N. cornutus	0(0)	65(63)	10(2)	5(1)	15(12)	10(15)	5(6)	5(1)	20(22)	0(0)	0(0)	(0)	20	1	9	17
S. atromaculatus	0(0)	17(1)	33(15)	0(0)	0(0)	50(54)	0(0)	0(0)	50(54)	17(29)	0(0)	(1)	6	1	6	12
N. rubellus	0(0)	8(2)	8(9)	62(64)	0(0)	0(0)	0(0)	23(1)	23(12)	0(0)	8(9)	(4)	13	0	9	4
C. perspicuus	0(0)	27(16)	2(5)	16(8)	2(3)	14(32)	10(17)	22(1)	45(64)	0(0)	0(0)	(4)	49	8	18	4
Diptera Feeders																
E. aestivalis	0(0)	4(1)	2(5)	8(7)	0(0)	0(0)	6(6)	62(1)	66(84)	0(0)	0(0)	(3)	50	9	16	4
P. mirabilis	0(0)	4(2)	0(0)	17(18)	0(0)	0(0)	13(26)	50(1)	58(76)	0(0)	0(0)	(4)	24	9	10	3
Bottom Ooze Feeders																
H. notatus	50(87)	17(4)	0(0)	0(0)	0(0)	0(0)	8(6)	8(1)	17(8)	(0)0	0(0)	(1)	12	1	11	20
H. hankinsoni	50(100)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	2	1	2	45
C. anomalum	100(92)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	50(1)	50(8)	0(0)	0(0)	(0)	2	0	2	6
P. promelas	100(100)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	7	0	6	39

* Period from April 1 through May 31, 1947. Collections taken between 0800 and 2000. Water temperatures ranged from 41° F. to 66.5° F.; and water levels from 1.41 feet to 5.85 feet.

** Columns under heading "Aquatic nymphs and larvae" include Ephemeroptera nymphs, Trichoptera and Diptera larvae, as well as Coleoptera, Hemiptera, and others.

TABLE VI. *Comparison of food habits of the more abundant species of minnows, Des Moines River (High-water)**

Species of Minnow (Cyprinidae)	Percentage of fish containing item and (in parenthesis) percentage of total volume											Summary			
	Bottom ooze**	Plant material	Adult terrestrial insects	Adult and emerging Diptera	Corixidae	Ephemeroptera nymphs ****	Trichoptera larvae ****	Dipterous larvae ****	Aquatic nymphs and larvae ****	Earthworm (*Lumbricus* sp.)	Miscellaneous ***	No. fish examined	No. fish empty	No. collections	Avg. volume of food as percentage of digestive tract
Omnivorous															
N. deliciosus	9(4)	44(40)	13(13)	0(0)	4(3)	22(16)	4(8)	4(1)	26(26)	0(0)	(14)	23	6	7	8
Semi-Specialized															
N. spilopterus	0(0)	25(23)	25(46)	19(2)	0(0)	16(7)	3(2)	0(0)	19(9)	0(0)	(20)	32	4	8	14
N. dorsalis	0(0)	17(3)	33(78)	0(0)	0(0)	0(0)	0(0)	17(1)	17(3)	0(0)	(16)	6	1	4	5
N. cornutus	0(0)	25(7)	25(57)	0(0)	0(0)	13(33)	0(0)	0(0)	13(33)	0(0)	(3)	8	4	6	4
C. perspicuus	6(11)	22(2)	9(3)	6(1)	0(0)	6(5)	0(0)	3(1)	9(5)	22(42)	(36)	32	6	7	16
Diptera Feeders															
E. aestivalis	0(0)	5(1)	10(26)	14(7)	5(4)	19(30)	0(0)	14(1)	33(36)	0(0)	(26)	21	8	6	6
P. mirabilis	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	33(1)	67(13)	33(87)	(0)	3	0	3	7
Bottom Ooze Feeders															
H. notatus	40(86)	10(1)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(13)	10	3	7	13
C. anomalum	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	1	1	1	0
P. promelas	100(100)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	(0)	2	0	2	30

* Period from June 1 through July 10, 1947. Collections taken between 0800 and 1800. Water temperatures ranged from 56.5° F. to 77° F.; and water levels from 1.75 feet to 19.30 feet. (Minimum water level at which collections were taken was 3.97 feet and maximum 17.45 feet.)

** Diatoms not present or scarce.

*** Mainly terrestrial larvae.

**** Columns under heading "Aquatic nymphs and larvae" include Ephemeroptera nymphs, Trichoptera and Diptera larvae as well as Coleoptera, and others.

Principal Food Items

The abundant foods of the minnows are classified in this study under broad headings to facilitate presentation. The same food types do not necessarily appear in the Des Moines River throughout all seasons and in tables II–VI the food types are included only if they occurred in large enough quantities to be considered important in the diet.

1. *Plankton and bottom microflora*

Bailey and Harrison ('48) list the various insects common to the Des Moines River in Boone County; however, they make little mention of the bottom microflora and plankton. In conjunction with the present investigation a plankton and microflora study was conducted. A report of this study is being made elsewhere (Starrett and Patrick, Ms.) and will be discussed here only in relation to the Des Moines River fishery. The true plankton of the Des Moines is almost entirely composed of algae. The zooplankton is rather scarce in the river as compared to more sluggish and polluted streams (Kofoid, '08; Allen, '20). Entomostraca are almost entirely limited to late fall, winter and early spring, and appeared regularly in the winter collections when they composed 5 per cent of the plankton on the basis of count. These organisms are taken rather frequently in winter by most minnows. The central bigmouth shiner seems to show more of a preference for entomostraca than any of the other minnows. Occasionally a single copepod was noted in a summer plankton collection or in a minnow collected in the summer.

The food studies indicate that phytoplankton is of little importance as a direct food for the minnows. The spotfin shiner was found to feed occasionally on phytoplankton in the summer, almost exclusively *Microcystis aeruginosa* Kütz. Insect larvae, especially Trichoptera larvae of the family Hydropsychidae, are known to be plankton feeders (Ross, '44) and examination of several specimens from the Des Moines substantiates this. The Hydropsychidae form an important part of the summer diet of several species of minnows and through this indirect way the plankton is perhaps of importance to the minnows.

The bottom microflora or bottom ooze in the Des Moines is an important food item for four species of minnows. The bottom ooze is composed mainly of diatoms and is distinguished from plankton in the digestive tract by the presence of fine sand and in some instances mud. The volume of bottom ooze in the digestive tracts was found to decrease with a rising river and to increase with a falling

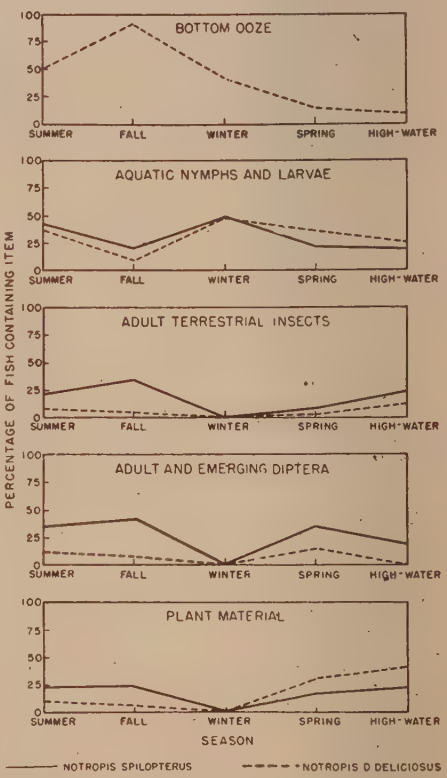

Fig. 3. Comparison of seasonal food habits of the Spotfin Shiner (*Notropis spilopterus*) and the Southwestern Sand Shiner (*Notropis d. deliciosus*) in the Des Moines River during 1946 and 1947.

river. During high water the bottom ooze feeders contained silt and mud with few or no diatoms. The bottom ooze feeders include: brassy minnow, bluntnose minnow, fathead minnow, and central stoneroller.

Dobie, Meehean, and Washburn ('48) state that the food of the brassy minnow is varied and these writers list animal plankton, plant plankton, aquatic insects, plants, surface drift, and silt as food taken by this minnow. Of the 34 specimens of brassy minnows examined from the river 31 contained bottom ooze and the remainder were empty. The specimens of fathead minnow examined contained only bottom ooze. Coyle ('30) in Ohio found that this minnow also takes some small aquatic insects. A specimen collected from a small tributary stream of the river contained dipterous larvae and no bottom ooze. This species was found by Kraatz ('23) in Ohio to be chiefly a bottom feeder with diatoms as a preponderant part of the diet. In the Des Moines River the bluntnose minnow was determined to be largely a bottom ooze feeder; however, its diet was found to be more varied than that of the other bottom ooze feeders. The specimens examined from the river tended to indicate that it is less of a general feeder here than Kraatz ('28) found in Ohio. The variations in the diets of these species as found in other localities tend to indicate that they are able to vary their diet to a limited extent depending on the amount of bottom foods present.

In addition to these four bottom ooze feeders, the southwestern sand shiner feeds to a considerable extent on bottom ooze. This species is quite omnivorous and seems to adjust its diet with the seasonal availability of food. With the fall decrease in available Ephemeroptera nymphs and Trichoptera larvae, the southwestern sand shiner diet was supplemented with bottom ooze. The ability of this shiner to use available foods is a possible contributing factor to its success in an environment subject to severe changes. This adaptability is further shown in its food habits during high water. In the absence or scarcity of true bottom ooze at high water stages, this shiner made use of the available plant material, terrestrial and aquatic insects.

Bottom ooze was found to be the chief food item taken by fry of the southwestern sand shiner, bullhead minnow, bluntnose minnow, and river carpsuckers (*Carpiodes* spp.). The fry of these species are present in August and September when the bottom ooze is usually rich in diatoms.

2. *Plant material*

The food class here designated as plant material does not include phytoplankton and bottom ooze. The following plant materials were taken most frequently by the Des Moines River minnows: germinated seeds of *Salix* sp., various seeds, fruits, and filamentous algae. The germinated seeds of *Salix* are available only in early summer and are fed on by all but the bottom ooze feeders. During this period 61 per cent of the spotfin shiners, excluding 0400 collections, contained *Salix* embryos which amounted to 53 per cent of the total volume of food. The other species of minnows tended to feed on the *Salix* embryos in lesser quantities. These *Salix* embryos evidently served to supplement the diminished available food supply through the high water periods in early summer of 1946 and 1947.

Filamentous algae are only occasionally taken by most minnows. The northern common shiner was found to contain more filamentous algae than any of the other minnows, largely in the summer and fall. Filaments of *Cladophora* spp. were the most frequent genus of algae in the fish examined. The filamentous algae in the river are found attached to rocks and sticks, and in this habitat there are several species of Heptageniidae and Baetidae nymphs. In some instances the algae in the fish may have been ingested accidentally while feeding on these nymphs.

Seeds and fruits occurred regularly in

the bullhead minnow and only occasionally in the other minnows. In the fall of 1946 a slight rise in water level covered some of the previous season's growth of *Eragrostis* sp., *Amaranthus* sp. and *Cyperus* sp. Seeds and fruits mainly of *Eragrostis* formed 69 per cent of the total volume of the bullhead minnow's fall diet. Other species of minnows collected with the bullhead minnow, including the spotfin shiner, southwestern sand shiner, bluntnose minnow, central bigmouth shiner, and northern common shiner, were seldom found to have taken seeds and fruits. The bullhead minnow in this instance was selective in its feeding and also was found to take seeds and fruits whenever available in other seasons.

3. *Terrestrial invertebrates*

Minnows in the Des Moines River feed upon terrestrial insects belonging to the following families: (Orthoptera) Locustidae, Gryllidae; (Neuroptera) Chrysopidae; (Hemiptera) Miridae, Lygaeidae; (Homoptera) Cicadellidae, Aphidae; (Coleoptera) Carabidae, Staphylinidae, Tenebrionidae, Elateridae, Anthicidae, Scarabaeidae, Chrysomelidae, Rhyncophora, and Curculionidae; (Hymenoptera) Formicidae, Ichneumonidae, and Pompilidae. Although nets were not set in this study as described by Needham ('28) to determine the amount of "drift food," field observations indicated an increase in abundance of this food in the presence of a wind and in the autumn. The vegetation, particularly overhanging trees, is undoubtedly an important source of this supply of food. The small adult terrestrial insects were taken more by the minnows in the fall than at other seasons. The spotfin shiner, rosyface shiner, central bigmouth shiner, and northern common shiner tend to feed at and near the surface more than the other common minnows. The increased feeding on terrestrial insects in the fall seems to be associated with the abundance of these insects and with the reduction in Ephemeroptera nymphs and Trichoptera larvae. Terrestrial insects, particularly Coleoptera, are of some importance in late spring and early summer high-water periods. Even the aquatic larvae feeder, the speckled dace, occasionally took a small adult terrestrial insect during high water.

Terrestrial Coleoptera and Lepidoptera larvae are taken by the minnows when available to them, as was found in the spring of 1947. For a period of a few days Lepidoptera larvae of the family Phalaenidae appeared in the diet of four species of minnows. These larvae constituted a main part of their diet while available. In high water terrestrial larvae are taken in the backwaters. Also some species of minnows take earthworms over the flooded land. These items might be considered as supplementary food during a period of adverse conditions.

4. *Aquatic nymphs and larvae*

Throughout the year aquatic nymphs and larvae form an important part of the diet of those Des Moines River minnows which are not strictly bottom ooze feeders. The Ephemeroptera nymphs and Trichoptera larvae comprise much of the summer diet. A reduction in volume of this fauna is expected following the emergence of the larger forms through the summer months. This reduction was not only reflected in the diet of the minnows but in the bottom samples as well. The small size of the young nymphs makes them rather inaccessible for most of the minnows. Both the fossorial and sprawling types of Ephemeridae nymphs are taken by the minnows in the summer. The genus *Ephoron* was almost limited to the summer diet. This fossorial nymph appeared to be taken by the minnows just prior to its transformation to the subimago stage. The sprawling type nymph *Potamanthus* occasionally occurred in the diet throughout the year. The Heptageniidae and Baetidae nymphs were found in the minnows at all seasons. The genus *Stenonema* appeared to be the most abun-

dant of the family Heptageniidae of mayfly nymphs in the river and occurred more frequently in the minnows. In the family Baetidae, *Baetisca* and *Blasturus* were abundant in the river but occurred rather infrequently in the diet of the minnows.

The family Hydropsychidae was the common form of Trichoptera larvae taken by the minnows in the summer of 1946. These larvae are found in the river attached to stones and sticks in the presence of current. In swifter waters they are often associated with the larvae of Simulidae. The Trichoptera larvae formed only a small part of the minnows' diet in the fall, winter and spring.

In the Des Moines River various dipterous larvae are available as food to fishes throughout most of the year. The Tendipedidae (= Chironomidae), Dolichopodidae, Tipulidae, and Ephydridae are the most important families of Diptera larvae. Simulidae were seldom taken by the minnows and appeared to be of more importance to the darters, which feed in the swifter water. The availability of larvae tends to be lessened during periods of high water as is clearly evidenced by table VI. Because of their small size and the more rapid rate at which they are digested (Raney and Webster, '40) one is apt to minimize the importance of Diptera larvae as a fish food. They form an important part of the annual diets of the speckled dace and suckermouth minnow. Dipterous larvae were found to comprise much of the diet of young spotfin shiners and northern common shiners. The other minnows took dipterous larvae in numbers only during the winter. In winter and early spring these larvae [4] formed a large percentage of the diet of ten of the common minnows based on occurrence rather than volume. Breder and Crawford ('22) found that *Notropis cornutus* in the Oxun River, D. C., fed more on Ephemeroptera and Plecoptera nymphs during the winter than other parts of the year. The northern common shiner (*Notropis cornutus frontalis*) in the Des Moines River was found to increase greatly its diet on dipterous larvae during the winter. Some Ephemeroptera and Plecoptera nymphs were taken in winter though in smaller quantities than in summer.

It is doubtful that the increased feeding on dipterous larvae in the winter of 1946–47 by ten species of the common minnows resulted in severe intra- and interspecific competition. Although no quantitative bottom samples were taken in the winter, inspection of sticks and rubble indicated a fairly abundant population of dipterous larvae. Also it appears that if the dipterous larvae had been depleted through the earlier part of the winter these forms would not have continued to compose a large percentage of the diet on up into early spring. Other aquatic nymphs and larvae, bottom ooze and entomostraca were present and served as supplementary foods.

Plecoptera nymphs were occasionally taken by minnows. *Taeniopteryx maura* (Pictet) nymphs are a part of the Des Moines River winter fauna, and are sometimes fed upon by the minnows. The smaller nymphal forms of *Acroneuria* spp. occurred infrequently in the minnows at other seasons. The large size of the Plecoptera nymphs prevents most of the minnows from taking them. This order of insects may be considered of little importance to the minnows in the Des Moines River.

Other nymphs were seldom found in the Des Moines River and were rarely taken by minnows.

[4] The winter and early spring dipterous larvae were largely *Cricotopus* sp. of the family Tendipedidae. This genus is also an important food item during other seasons. From the fall and summer collections the following dipterous larvae appeared as food items: *Bezzia* or *Protobezzia* sp., *Cryptochironomus* sp., *Hydrophorus* (similar), and *Cricotopus bicinctus* Meig. This material was checked by Mr. A. R. Brooks, of the Department of Agriculture of Canada.

5. *Adult and emerging Diptera*

The emerging and adult Diptera[5] are an important food of the spotfin shiner and central bigmouth shiner in the fall. These fishes appear to feed more at the surface in the fall than in other seasons. This is further evidenced by the increase in terrestrial insects in their diet through this season. The rosyface shiner also followed this trend.

Discussion

It is of some interest to compare the feeding trends of the spotfin shiner and southwestern sand shiner, the two most abundant species of minnows in the river (fig. 3). The competition, if any, between these two species appears to be quite limited in the presence of many food items. In the summer these two species as well as others feed on aquatic nymphs and larvae; however, through this season there were other available or supplementary food items, such as terrestrial insects, emerging and adult Diptera, bottom ooze, filamentous algae, and adult aquatic insects. In the winter the spotfin shiner and southwestern sand shiner fed to a large extent on dipterous larvae. As stated above this was a common trend for most of the minnows. In winter some competition among species might exist for dipterous larvae, particularly if the environment had been unfavorable to dipterous production the preceding year. The absence of terrestrial insects and emerging aquatic insects in the winter reduces the amount of available supplementary foods. The spotfin shiner and southwestern sand shiner were able in the fall of 1946 to compensate for the shortage of aquatic nymphs and larvae in their diets. The spotfin shiner did this with terrestrial insects and emerging and adult Diptera, whereas the southwestern sand shiner increased its feeding on bottom ooze. It is difficult to establish definite interspecific competition of fishes for food. Lagler ('44, p. 213) in discussing this problem states:

> "The mere fact that two or more species feed upon the same organism or group of organisms cannot be taken as direct evidence that an evil exists. For if the food item is abundant it is possible that the feeding could have little effect on the supply."

In case of the two abundant shiners in the river it is doubtful if severe interspecific competition exists except possibly in the winter and early spring. This possibility is slight since food requirements during cold months are probably at a minimum. From the data on these two minnows the writer is led to believe that these fish tend to change their diet to other abundant foods when available rather than enter into severe competition.

Only three species of minnows had eaten fish. The river shiner preys on minnows to some extent in the fall. This species was rather scarce in the river and it is doubtful that its predation had any effect on the population. The northern common shiner and the northern creek chub in summer fed largely upon aquatic nymphs and larvae, plant material and adult terrestrial insects. The northern common shiner also ate bottom ooze, an item which was not taken by the chub. With the fall decrease in aquatic nymphs and larvae, both species started to eat minnows. The availability of minnows was much greater in the fall of 1946 than in the preceding summer. The abundance of young southwestern sand shiners coupled with their tendency to form large concentrations in the fall perhaps made them quite vulnerable to the larger minnows and other fishes. The common shiner compensated for part of this fall decrease in aquatic insects by taking more bottom ooze, but the chub did not. In the fall, bottom ooze amounted to 2 per cent of total food volume in the northern creek chub as compared to 34 per cent in the northern common shiner. The northern creek chub's diet in the fall became mostly minnows amounting to 70 per cent

[5] The adult and emerging Diptera included the following families: Tendipedidae, Sciaridae, Tipulidae, Empididae, Dolichopodidae, Syrphidae, Culicidae, Cecidomyiidae, and Tachinidae.

of the volume. It appears that the aquatic nymphs and larvae are possible buffers for the smaller minnows in late summer. In winter some predation existed on the smaller minnows by the northern creek chub and northern common shiner. In the spring of 1947 the northern common shiner's diet was chiefly plant material including buds and algae, and no specimen examined contained minnows. The northern creek chub continued to prey on minnows in the spring.

The southern channel catfish (*Ictalurus lacustris punctatus* (Rafinesque)) is the only abundant large predatory fish in the river. Bailey and Harrison ('48) made a detailed study of the food habits of this fish in the Des Moines River, Boone County, Iowa. They found the food of the young to be mainly dipterous larvae, with lesser amount of Ephemeroptera nymphs and Trichoptera larvae. These food items also make up a large part of the minnow's diet in summer. The speckled dace and suckermouth minnow are mainly dipterous larvae feeders and it appears that some competition might exist among these strict feeders and the young catfish, particularly if all three species were very abundant.

Ephemeroptera nymphs and Trichoptera larvae were found by Bailey and Harrison to be taken more by the larger catfish. The insect-feeding minnow's diet in summer was partially composed of these aquatic nymphs (table II). The channel catfish appears to have a varied diet and apparently is able to change its feeding as certain food items become abundant or rare.

The ability of certain fishes to modify their diet to take abundant foods and to compensate for the absence of their usual food items is probably an important factor in regulating the abundance of various species. The turbidity of the water and the scarcity of food makes the high-water stage a critical period for fish, particularly for young of the year. Forbes ('83) in discussing the food habits of smaller fresh-water fishes mentions that the young Cyprinidae draw almost indiscriminately for their food supply upon protozoa, algae, and entomostraca. Forbes ('80, p. 77) states that

> "Running water is relatively destitute of Entomostraca, and hence fishes denied access while breeding to slow or stagnant water in which Entomostraca abound, have no chance to multiply."

The scarcity of entomostraca may be a limiting factor for some species of fish in the river. According to Bajkov ('32) one of the causes of great mortality of fry is the lack of food, especially plankton organisms. The plankton studies on the Des Moines River indicate the sarcity of true plankton in late spring during high river stages. The fluctuating waters in the spring also tend to reduce the bottom microflora. The young of yellow pike-perch (*Stizostedion v. vitreum* Mitchill) are known to feed on entomostraca (Smith and Moyle, '45). The few young of this species taken in the river in late May and early June were all empty. The scarcity of entomostraca in the river through this period may be a limiting factor for this fish. Other spring and early summer spawners in the river may also be limited by the scarcity of zooplankton for the fry and fingerlings. The western golden shiner occurred in only two Des Moines River collections. According to Hubbs and Cooper ('36) this species prefers weedy lakes. The Des Moines River may not provide the proper habitat for this shiner, since it lacks entomostraca. The main food elsewhere for the golden shiner is entomostraca as summarized by Hubbs and Cooper ('36). The common emerald shiner shows a preference for lakes (Eddy and Surber, '47), and in Lake Erie Ewers ('33) found two-thirds of the volume of its summer food is plankton crustacea. Forbes and Richardson ('20) in Illinois found that it feeds on insects, algae, minute fish, and entomostraca. This species occurs in only small numbers in the Des Moines. Only five specimens were ex-

amined and were found to contain aquatic nymphs and larvae and terrestrial insects. Perhaps the scarcity of entomostraca as food is unfavorable also to the common emerald shiner in the Des Moines.

Summary

The food habits of 13 common minnows (Cyprinidae) in the Des Moines River, Boone County, Iowa, were studied to determine food relationships among the various species.

The minnows in the Des Moines River may be classed as specialized feeders and as general feeders. The general feeders are capable of modifying their feeding habits and thus avoid serious competition. Food may limit the abundance of the specialized feeders and the fry and fingerlings of other species.

Four species of minnows fed almost exclusively upon the bottom ooze which was composed largely of diatoms. Two other species were primarily dependent upon the larvae of Diptera and other insects.

The non-specialized feeders were found to adjust their feeding habits to the seasonal changes in the abundance of various food items.

Severe interspecific competition for food was not thought to exist among the minnows during the course of this investigation. Some competition possibly existed in the winter of 1946–47 for dipterous larvae; however, it appears that the abundance of the dipterous larvae, other compensating foods, and diversified feeding habits of the minnows reduced the competition to a minimum.

The scarcity of entomostraca, bottom microflora, small dipterous larvae, and turbidity of the water during periods of high water in late spring and early summer are believed to be limiting factors for certain fishes in the river.

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MAJOR PLANT COMMUNITIES OF TENNESSEE CEDAR GLADES

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Physiographically the middle portion of Tennessee is a basin surrounded by the rim of the Interior Low Plateau. Although the entire Central Basin is calcareous, cedar glades occur only on Lebanon limestone, of the Stones River Series, a dolomitic rock of Ordovician age. There are approximately 300 square miles of this Lebanon stone which is fairly well distributed throughout the basin (fig. 1). It is horizontal, thin bedded and deeply cracked vertically in many places.

The "glades" are open spaces occasioned by the presence of rock at or near the surface. They may be simply exposed rock surfaces or gravelly or grassy expanses surrounded by cedar woods. Six kinds of areas were selected as typical of glade regions: rock, gravel and grass glades, shrub thickets, cedar and cedar-hardwood stands. Examples of each of these were sampled in an effort to obtain a fairly complete picture of the structure and composition of these communities and to show the successional relationships among them.

METHODS

Vegetation on rock

Plant succession upon Lebanon limestone was studied intensively in three glades in Davidson and Rutherford Counties and conclusions verified by observations of vegetation on glade rock throughout the Central Basin. Representative mats were mapped and photographed and transects were charted to show zonation. An inferred successional pattern was arrived at by comparing mats of various sizes, depths and zonations.

The same general plan of study was used in determining succession of plants in crevices.

Vegetation on soil

After a general survey of glade regions, communities were selected for phytosociological study by the quadrat method. All areas studied were on soil over glade limestone, which forms Hagerstown stony loam (Ayrs and Gray, '07). The areas selected were level or nearly so, thus obviating consideration of topographic differences.

Nested quadrats of three sizes (10 × 10 m, 4 × 4 m, 1 × 1 m) were used in much the same manner as described by Oosting and Billings ('39). In the 10 square meter size, all trees over 1 inch d.b.h. or over ten feet tall were counted, diameters measured and crown cover of each species estimated. Records were kept separately for over- and understory. In the 4 square meter quadrats shrubs and transgressive trees, that is, young trees which may ultimately become part of the under or overstory canopy, were counted. These were recorded as over and under 1 foot in height, and cover of each species was estimated. Specimens were collected from the ground layer in these plots and per cent of cover estimated for each species insofar as field recognition was possible. Lists were completed after laboratory determination of specimens. In this way, six layers of the wooded communities were sampled. In open communities, as many as were present of these six layers were sampled in the same way. Ten sets of quadrats were used in each instance and spacing was determined by the shape and size of

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the stand to be sampled. Quadrats of the 4 square meter size were used in open glades, and all three sizes in the shrub and tree stands.

Number and size of quadrats for all layers of each community proved adequate when tested by species: area curves (Cain, '38). The curves constructed from data from the 1 square meter quadrats (herbs) did not break as sharply as the others but this might be expected because of the gradual inclusion of many

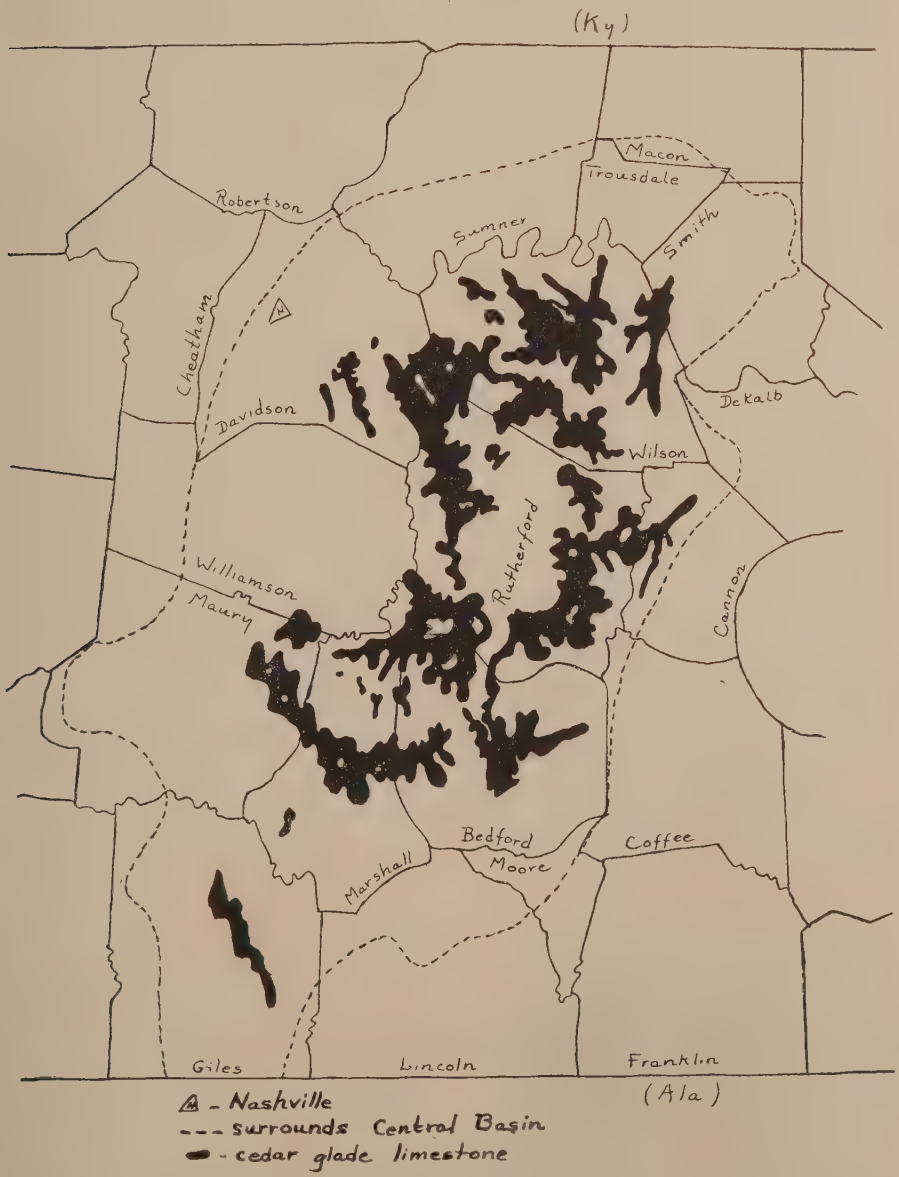

FIG. 1. Map of middle Tennessee showing location of cedar glades.

species that are very irregularly dispersed. A safe margin was indicated even in these.

Soil

Soil samples were collected in duplicate from each station once a week from March 20 to June 5, 1947. One additional collection was made at most of these stations on May 27, 1948, after ten days of drought. The difficulties involved in taking cores of the rocky soil made it impractical to get undisturbed samples. Collections were made with a soil auger and the samples placed immediately in tightly closed containers. Only the A horizon could be reached except in the cedar-hardwood stand whose B horizone was also sampled. At the other stations, rock lay a few inches below the surface so the accumulation layer, if present at all, was in the seams of rock. Depth of soil was noted with each sample.

Soil moisture content was determined by weighing, drying to constant weight at 100° to 105° C and calculating the moisture content in terms of dry weight of the soil. Wilting percentage of soil from each station was obtained by using phytometers, and available moisture then calculated by subtracting the wilting percentage from the total amount of moisture in each collection. Maximum water retaining capacity, capillary capacity and pore space were determined for the soil from each station. Loss on ignition was used as an approximation of the amount of humus present in each soil.

Results

Vegetation on rock

Successional development of vegetation in the glades occurs differently on shaded and unshaded rock surfaces, in crevices of rock glades and on small, isolated flat rock exposures.

Unshaded rock surface.—Slight depressions that are frequent in the surface of Lebanon limestone collect small quantities of mineral soil and gravel. Little moisture is retained but soil is important in initial succession on unshaded rock glades. No mats were found forming from vegetation established directly upon rock surfaces, but colonies of blue-green algae, usually including species of *Oscillatoria, Stigonema, Scytonema* and *Nostoc,* were found consistently on shallow soil in depressions and mats develop upon these. The algae form a dark, felt-like layer that is conspicuous when wet, but is easily overlooked when dry. This algal crust curls up as it dries, especially along the edges of mats. *Nostoc commune* Vauch[1] grows abundantly in broad flat strips that form conspicuous moist masses or crisp dry fragments over the surface of shallow soil or bare rock. Such lichens as *Dermatocarpon hepaticum* (Ach.) T. Fries,[2] *Leptogium tremelloides* (L.) S. F. Gray and *L. dactylinum* Tuck, are frequent on mats in early stages of development.

A small succulent, *Talinum teretifolium* Pursh., is the first perennial seed plant that becomes established on soil in depressions (fig. 2). *Sedum pulchellum* Michx. is abundant in such depressions in the spring, and its stiff dead stalks catch wind and water-drifted sediment through the following summer, thus adding material to the mat.

Grimmia apocarpa Hedw. and occasionally a *Bryum* species invade the *Nostoc-Talinum* zone and form the next distinct stage of mat development. On small mats and on the uphill side of larger ones, mosses become so covered with silt that only a few tips of the plants are exposed. This accumulation, of course, adds to the width and depth of the mat. Although neither *Grimmia* nor *Bryum* was found growing directly upon rock, after either enters a mat, it spreads gradually over the adjoining rock surface. *Talinum* remains as an associate of the *Grimmia,* not restricted to that zone but thriving upon it.

[1] Authorities are given the first time a plant name is mentioned and omitted thereafter.

[2] All lichens determined by G. G. Nearing.

FIG. 2. *Talinum teretifolium* and *Sedum pulchellum* on a *Nostoc commune-Leptogium dactylinum* layer. *Leptogium* is unusually abundant here.

By accumulation of organic matter and soil, mats gradually deepen and widen. *Nostoc* and *Talinum* spread onto the shallow margin as the mat advances and the deeper soil is invaded by herbs, mostly *Petalostemum Gattingeri* Heller and *Erigeron ramosus* (Walt.) B.S.P. Simultaneously with the herbs, *Pleurochaete squarrosa* (Brid.) Lindb. covers the ground layer of the deeper zone and spreads onto the surrounding *Grimmia*. If shaded enough, it extends to the margin of the mat and invades the rock to some extent.

These three more or less concentric zones, *Nostoc-Talinum, Grimmia,* and *Erigeron-Pleurochaete,* show clearly in figure 3.

The herb zones of deeper mats are invaded by one or more of the typical glade shrubs, *Rhus aromatica* Ait., *Forestiera ligustrina* (Michx.) Poir. or *Symphori-*

FIG. 3. Mat showing three zones; gravelly outer zone with *Nostoc* and *Talinum* present, dark *Grimmia* zone and inner zone of herbs (*Erigeron ramosus* and *Bromus japonicus*).

carpus orbiculatus Moench. Seedlings of *Ulmus alata* Michx., *Celtis laevigata* Willd. and *Juniperus virginiana* L. become established on mats but if they grow to tree size they are likely to be rooted in vertical crevices as well as in the soil of a surface mat. *Pleurochaete squarrosa* remains the most important species of the ground cover under shrubs and trees until shade becomes very dense.

Many additional species may be found in the zones representing the first three stages of development. The *Nostoc-Talinum* zone often includes *Physcomitrium turbinatum* (Michx.) Brid., *Archidium ohioense* Schimp., *Astomum ludovicianum* Sull., *Riccia macallisteri* Howe, and *Dermatocarpon* spp. *Desmanthus illinoensis* (Michx.) MacM., *Croton monanthogynus* Michx., *Scutellaria parvula* Michx. and *Opuntia Rafinesquii* Engelm. are frequent associates of the dominants in the *Erigeron-Pleurochaete* zone. *Opuntia* may also start on *Grimmia*. *Arenaria patula* Michx. and *Leavenworthia* spp. are abundant in early spring on all three zones of shallow mats.

Shaded rock surface.—In partly shaded

areas like the flat blocks of limestone between lines of mature trees, pioneer mosses occur directly upon the rock . On the flat, upper surfaces of such blocks, *Orthotrichum strangulatum* Schwaegr. is the only important pioneer (fig. 4). Small plants spread centrifugally, becoming tufts 2 or 3 inches in diameter. These tufts are invaded by *Pleurochaete squarrosa*. As long as the crown cover of the stand is somewhat broken *Pleurochaete* persists, but in heavier shade, dominance shifts to *Thuidium recognitum* (Hedw.) Lindb. directly or to *Entodon seductrix* (Hedw.) C. Mull. followed by *Thuidium*.

Pleurochaete, Entodon or *Thuidium* may be invaded by *Climacium americanum* Brid. (fig. 5). In old, mature cedar

FIG. 4. Pioneer tufts of *Orthotrichum strangulatum* on partly shaded limestone.

woods *Climacium* forms a large part of the ground cover and is as typical of subclimax stands as is red cedar (fig. 6).

Several species may occur directly on small ledges and vertical sides of the cracks. The most common of them are *Tortella flavovirens* (Bruch.) Broth., *Grimmia apocarpa gracilis* (Schl.) W. & M. and *Orthotrichum strangulatum*. These moss mats are usually invaded by *Entodon* or *Thuidium* and occasionally by *Anomodon rostratus* (Hedw.) Schimp or *A. minor* (Beauv.) Lindb. which is then followed by *Thuidium*. *Pleurochaete* and *Climacium* are common only on the flat surfaces but *Thuidium* is frequent on sides of cracks as well.

Aquilegia canadensis L., *Woodsia obtusa* (Spreng.) Torr., *Asplenium platyneuron* (L.) Oakes, *Pellaea atropurpurea* (L.) Link., *Asplenium resiliens* Kuntze and other herbs typical of cedar woods become established on shaded moss mats. Tree seedlings start here also but often die in the shallow soil. It is conceivable that, in time, sufficient soil may accumulate on such surfaces to support tree growth, but this has not happened in the stands investigated.

Cladonia spp., mostly *C. furcata* (Huds.) Schrad. and *C. turgida* (Ehrh.) Hoffm., are frequent on moss mats in shade and *Dicranum scoparium* Hedw. is occasional. These species are not an essential part of succession on rock.

Where a fair amount of sunlight reaches the rock, *Pleurochaete* mats develop, either on *Orthotrichum strangulatum* or upon masses of *Nostoc commune* in depressions. Later moss stages do not appear and seedlings of *Opuntia, Arenaria, Sedum, Satureja glabella* (Michx.) Briquet and other herbs become established and are later succeeded by the same species of shrubs that occur in sunny glades.

Cracks in rock.—One of the most important vegetational developments that occurs on glade limestone is that which takes

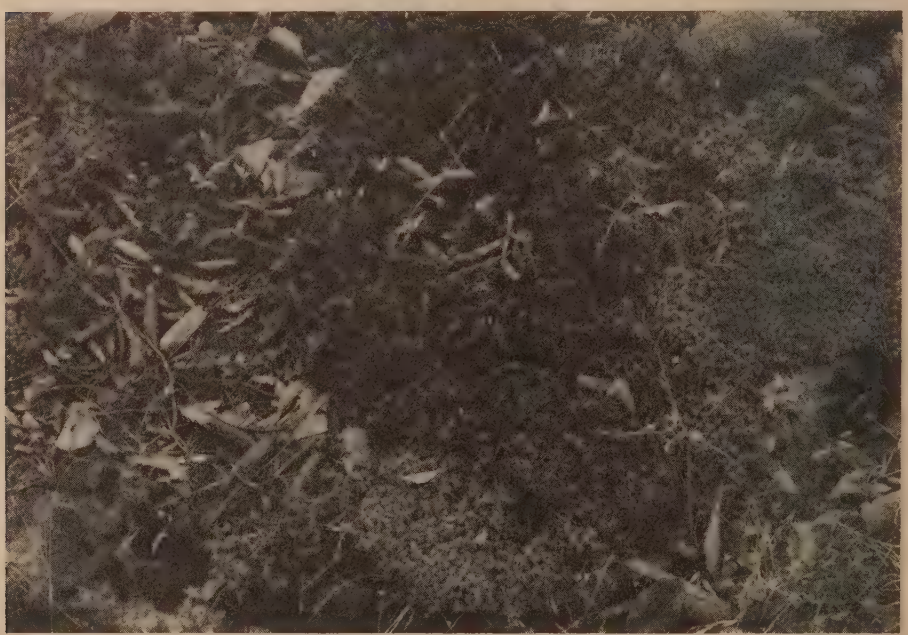

FIG. 5. Close-up of three stages in bryophyte succession on shaded rock. Black *Orthotrichum* tufts on rock at lower left being covered by *Pleurochaete*, which is in turn invaded by *Climacium americanum*.

FIG. 6. Cedar sub-climax stand. Succession on shaded rock has been in progress some time. Note trees are in cracks only—flat surfaces are rock covered with shallow mats.

place along vertical cracks in the rock. Such cracks are of varying widths and depths but usually quite long. They may extend more or less parallel to each other across an open glade or intersect at right angles, separating the rock into large rectangles like sidewalk sections (fig. 7). The first type leads to open, soil-covered glades separated from each other by lines of trees and shrubs; the second develops into woods containing large blocks of limestone such as were described under "shaded rock surface."

The first stage in vegetational development along cracks is dominated by herbs. Any of the species common in open glades and a number of weeds are able to exist in crevices. Determination of pioneer species, therefore, is probably related to seed source.

Crevices originally occupied by herbs widen and fill with soil. These slightly wider cracks are occupied by shrubs. *Forestiera, Rhus* and *Symphoricarpus* are the most frequent dominants in this stage. The first trees that become established, *Juniperus virginiana, Ulmus alata* and *Celtis laevigata,* eventually develop into cedar sub-climax woods.

Small, isolated flat rocks: Small areas of rock frequently remain exposed in an otherwise soil-covered glade and show interesting variations from the usual successional pattern. Invaders are the species of the ground cover of the immediately surrounding soil. They vary according to the stage to which the glade as a whole has progressed and to the particular combination of species that compose the ground cover.

Vegetation on soil

In the statistical results of community studies, density indicates the average number of individuals on the plots used in sampling each stand (Braun-Blanquet, '28). Frequency refers to the percentage-frequency of Raunkiaer ('34), that is, number of plots containing individuals of a species expressed as a per cent of the

FIG. 7. Herb stage of succession along cracks.

total number of plots used in the stand. Frequency diagrams are based on five frequency classes after the plan of Raunkiaer ('34).

As mats of vegetation on unshaded rock gradually widen and merge with each other, a glade with shallow gravelly soil is formed. The same type of glade develops between parallel cracks in rock glades as wind and water drop sediment behind lines of vegetation in the cracks. In spring the soil of such areas is kept wet by frequent rains, but becomes extremely dry in summer and fall (Freeman, '33).

The only species of any importance in the ground layer in gravel glades is the ever-present *Nostoc commune*. Such mosses as *Archidium* spp. were collected from glades of this type, but none were present in the quadrats. The most conspicuous species in gravel glades are spring dominants. *Leavenworthia* spp., *Arenaria patula, Sedum pulchellum* and *Psoralea subacaulis* T. & G. are aspect dominants that disappear by the time the soil dries out. *Petalostemum Gattingeri* Heller and *Hypericum sphaerocarpum* Michx. are conspicuous in the spring and remain as two of the summer dominants. *Hypericum* occupies the slightly wetter parts of gravel glades and *Petalostemum* the drier. The spreading habit of *Petalostemum* gives it a physiognomic dominance, although *Aristida* and *Sporobolus* are dominants with a frequency of 100 per cent and 47 per cent coverage as compared with 70 per cent frequency and 2 per cent coverage of *Petalostemum*. Since it was not possible to distinguish *Aristida* from *Sporobolus* at the time of counting, data for the two were taken together. Occasional shrub and tree seed germinate but mortality is high during the summer drought. Some survive, however, as shown by the presence of a few *Celtis, Juniperus* and *Ulmus* seedlings and by scattered plants of *Forestiera, Rhus, Symphoricarpus* and *Rosa*. Soil develops by weathering of rock, decay of organic matter and deposition of erosion drift.

A grass stage dominated by *Aristida longispica* Poir. and *Sporobolus* sp. develops on those glades covered with about 3–6 inches of soil. Cover in the grass glade quadrats was 52 per cent *Aristida* and *Sporobolus*, the rest being made up of many species, no one of which occupied a great deal of space. *Petalostemum, Erigeron, Euphorbia dentata* Michx., *Ophioglossum Engelmannii* Prantl, *Croton monanthogynus, Psoralea subacaulis* and *Galium virgatum* Nutt. each had a frequency of 50 per cent or more. *Petalostemum* was still an important species but became crowded as grasses spread around it. *Panicum* spp. entered the grass glade and remained throughout the rest of the series. *Pleurochaete*, with a frequency of 70 per cent and a coverage of 7 per cent, was the only important species in the ground layer. *Nostoc commune* had a frequency of 60 per cent but its coverage was less than on the more sparsely covered gravel glades. Species of *Petalostemum, Psoralea, Phlox, Delphinium, Oxalis* and *Lobelia* are common spring aspect dominants.

Tall herbs, chiefly *Erigeron ramosus, Grindelia lanceolata* Nutt., *Ratibida pinnata* Barnh. and *Rudbeckia triloba* L., frequently appear with *Aristida* and *Sporobolus* in the grass stage and might be considered successional if such a stage were consistently present. *Rudbeckia triloba* is usually found in slightly wetter glades than the others.

In quadrats in the grass glades, *Erigeron* had a frequency of 70 per cent and a coverage of 2.5 per cent; *Grindelia* a frequency of 20 per cent and a coverage of 1 per cent; no *Ratibida* was present in this stand. *Erigeron ramosus* is used in discussion as representative of the tall herb stage, since it was the species most frequently present in the sample plots. Zonation of herbs and occurrence of aspect societies are caused by variations in depth of soil and in moisture relations (Freeman, '33) and by shade.

The beginning of a shrub layer is evident in grass glades, suggesting that shrub

thickets may eventually form there. *Rosa carolina* L. and *R. setigera* Michx., *Forestiera* and *Symphoricarpus,* all of which occur in gravel glades, are present and show slight increases in frequency over gravel glade figures. Trangressives of *Juniperus, Celtis* and *Ulmus* were present in several quadrats but of no great importance as compared with herb dominants.

Thickets with small glades winding between clumps of shrubs indicate a gradual advance of woody vegetation into open glades. Data on such a glade-shrub stand show *Forestiera ligustrina* with a frequency of 90 per cent and a density of 5.6 per cent, and *Rhus aromatica* with a frequency of 90 per cent and a density of 8.7 per cent, to be dominants in the stand. *Forestiera* spreads vegetatively by layering of branches that droop and touch the ground. *Symphoricarpus,* not present in this stand but observed in similar ones, sends out runners that reach 10 to 15 feet. Both species have been observed encroaching in this way upon neighboring glades. The two rose species present in open glades and two common vines, *Smilax rotundifolia* L. and *Parthenocissus*

FIG. 8. Glade-shrub community with aspect society of *Delphinium virescens* in foreground and *Juniperus* seedlings showing above *Forestiera-Rhus aromatica* thicket.

FIG. 9. Fifty- to sixty-year *Juniperus* overtopping a *Forestiera-Rhus aromatica* thicket.

quinquefolia (L.) Planch., were also found in this stand.

Ground cover of the glade-shrub stand was very light: *Pleurochaete* had a coverage of 10 per cent and a frequency of 30 per cent and a number of species were included that are characteristic of later stages of development. *Aristida* and *Sporobolus,* frequency 80 per cent and coverage 11.5 per cent, and such common glade herbs as *Croton monanthogynus, Arenaria patula, Euphorbia dentata* and *Petalostemum* occupied space between shrub clumps, tying this stage to the preceding.

Well-established seedlings of cedar, winged elm and hackberry suggest possibilities of a future forest condition (fig. 8). Frequency and density of each of these species was greater than in open glades, and a few individuals of *Juniperus, Ulmus alata, U. fulva* and *Celtis* constitute more or less of an over- and understory of trees.

A stand of 50–60-year-old cedar overtopping a *Forestiera-Rhus aromatica-Symphoricarpus* thicket indicates the trend of development following a glade-shrub thicket (fig. 9). *Pleurochaete* forms a major part of the ground cover, its frequency being 90 per cent and its coverage 42.5 per cent. This is the peak of its development in the stands sampled.

Erigeron, Croton monanthogynus, Euphorbia dentata, Panicum flexile (Gatt.) Scribn., *Aristida* and *Sporobolus* in the herb layer may be considered remnants of an open glade condition.

A shrub layer with *Forestiera, Rhus* and *Symphoricarpus* as important species also included *Rosa carolina, Smilax* and *Parthenocissus.* With respect to both frequency and density *Juniperus* was the most important of the woody transgressives and of the understory. The overstory was made up of scattered cedar, winged elm, slippery elm and blue ash (*Fraxinus quadrangulata* Michx.).

In an 88-year stand, *Juniperus* and *Ulmus alata* were dominant in the over-

story. As transgressives *Ulmus alata* had a frequency of 90 per cent, *Juniperus* of 80 per cent and *Celtis* of 70 per cent, indicating a continuance of the same species in the dominant layer. However, the presence of *Quercus montana* Willd. and *Carya* spp., both with frequencies of 40 per cent, suggests that these hardwoods have a good chance of becoming part of the mature stand.

Forestiera, Rhus and *Symphoricarpus* have high frequencies in the shrub layer and enter the woody understory in several places. Several understory trees characteristic of glade woods, *Rhamnus caroliniana* Walt., *Bumelia lycioides* (L.) Gaertn. f. and *Fraxinus quadrangulata,* were present as transgressives in this stand.

Aristida and *Sporobolus* were again the most important species in the herb layer with a frequency of 30 per cent and a coverage of 5.3 per cent. The herb layer was thin in this stand and consisted of scattered individuals of 35 species. *Erigeron* and *Croton monanthogynus, Arenaria* and *Euphorbia dentata* reflect the open glade condition, while *Galactia mississippiensis* (Vail) Rutgers, *Geum, Galium pilosum* Ait. and *Sanicula* are more characteristic of glade woods.

Pleurochaete squarrosa covered 13.1 per cent of the ground surface, and *Cladonia furcata* with an 80 per cent frequency and *C. subcariosa* Nyl. with a 40 per cent frequency are conspicuous parts of this layer.

In a 103-year stand (fig. 10) cedar was distinctly dominant. In the overstory it had a frequency of 90 per cent and a density of 7.4 per cent, while the next most important species, *Ulmus alata,* had a frequency of 30 per cent and a density of 0.5 per cent. In the understory the frequency of *Juniperus* was 100 per cent and its density 0.6 per cent. *Ulmus*

FIG. 10. Interior of 103-year cedar stand. Note young hickory at left and *Fraxinus quadrangulata* at right.

FIG. 11. Interior of cedar-hardwood stand. Chestnut oak at right center and hickory seedlings in ground layer.

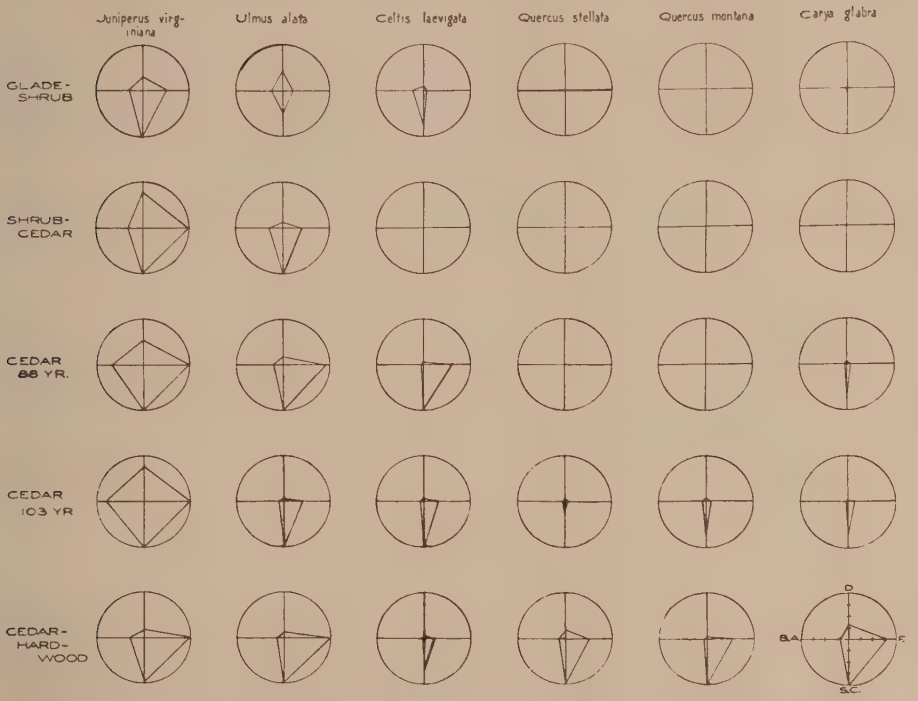

FIG. 12. Phytographs of dominants and sub-dominants in shrub and forest stands.

alata, Juniperus and *Celtis* had the greatest density and frequency of transgressives in this stand. *Rhamnus, Cercis, Bumelia* and *Cornus* as transgressives indicate the possibility of a distinct layer of understory species as the stand matures. Transgressives of *Quercus montana, Q. velutina* Lam. and *Carya glabra* (Nutt.) Nees. may be interpreted as indicators of a slightly more mesic condition than a *Juniperus-Ulmus-Celtis* woods.

Forestiera, Rhus aromatica and *Symphoricarpus* were again among the chief constituents of the shrub layer, which also includes *Rosa carolina* and *Hypericum frondosum* Michx. Vines were present in greater abundance than in younger stands.

Open glade herbs present in this stand were *Croton monanthogynus, Erigeron, Aristida* and *Sporobolus, Panicum flexile* and *Ophioglossum.* None except the grasses was of much importance in terms of frequency or coverage. *Galactia, Geum, Galium pilosum* Ait. and *Sanicula* which are common species of glade woods all reach their peak of frequency in this stand.

Pleurochaete, in 80 per cent of the quadrats and with a 30 per cent coverage, was the most important species in the ground cover. *Cladonia furcata* was in 70 per cent of the sample plots, but its coverage was only 1.5 per cent. The few other species present had frequencies of 10 per cent each.

A cedar-hardwood stand on glade soil (fig. 11) was interpreted as an indication of a trend toward the mesophytic regional climax. *Juniperus* and *Ulmus alata* were dominants in the overstory, but there were also individuals of *Carya glabra, Juglans nigra, Quercus stellata* Wang, and *Q. velutina* in that layer. The same hardwoods were well represented in the understory. Frequencies of transgressives of

Carya glabra, Quercus montana, Q. velutina and *Q. stellata* compare favorably with those of *Juniperus, Celtis* and *Ulmus*. None of these is dominant in the regional climax but the appearance of species somewhat more mesophytic than cedar suggests the possibility of a still greater change toward mesophytism in the future.

Most of the shrub species that were in the cedar stand were present in the cedar-hardwood stand, with the addition of *Lonicera sempervirens* L.

A few scattered open glade herbs were present, *Panicum flexile* being the only one there with any degree of regularity. For the first time, no *Aristida* or *Sporobolus* was listed in the quadrats, but many species typical of glade woods were present. *Helianthus hirsutus* Raf. and *Solidago ulmifolia* Muhl. that were found here were not observed in glade woods at all.

For the first time since grass glades no *Pleurochaete* was found in the sample plots, but both *Cladonias* were present. *Plagiothecium, Cirriphyllum, Anomodon* and several species of *Fissidens* present in the ground cover are also common in hardwood stands throughout the region.

Phytographs (fig. 12) show the relative importance of tree dominants and subdominants in shrub and forest stands. Red cedar is clearly dominant in all stands —all classes are represented in each stand and frequency and basal area are con-

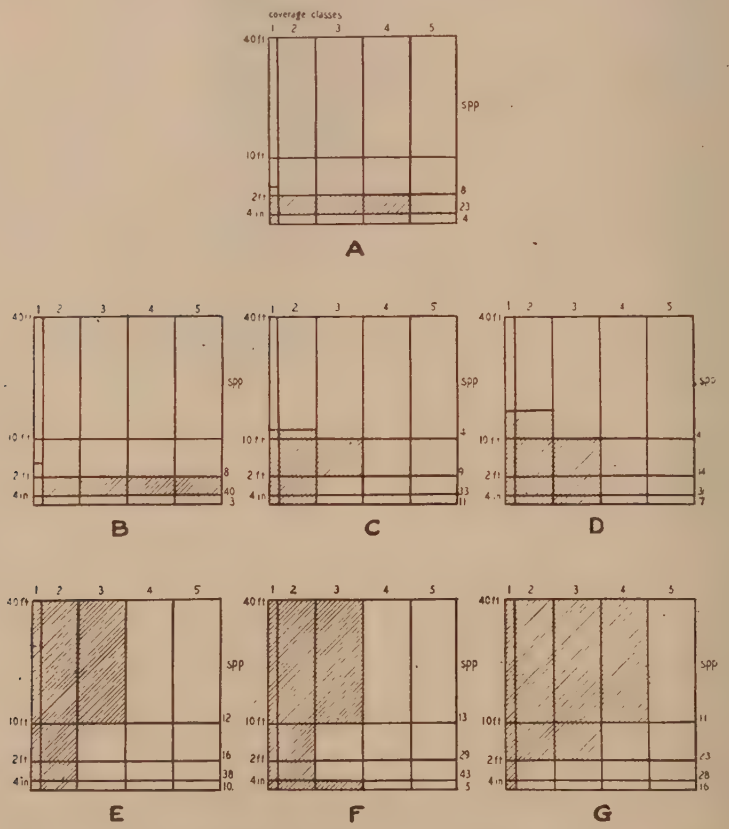

FIG. 13. Cover-stratification of glade and glade woods communities. A—gravel glade; B—grass glade; C—glade-shrub; D—shrub-cedar; E—88-year cedar; F—103-year cedar; G—cedar-hardwood.

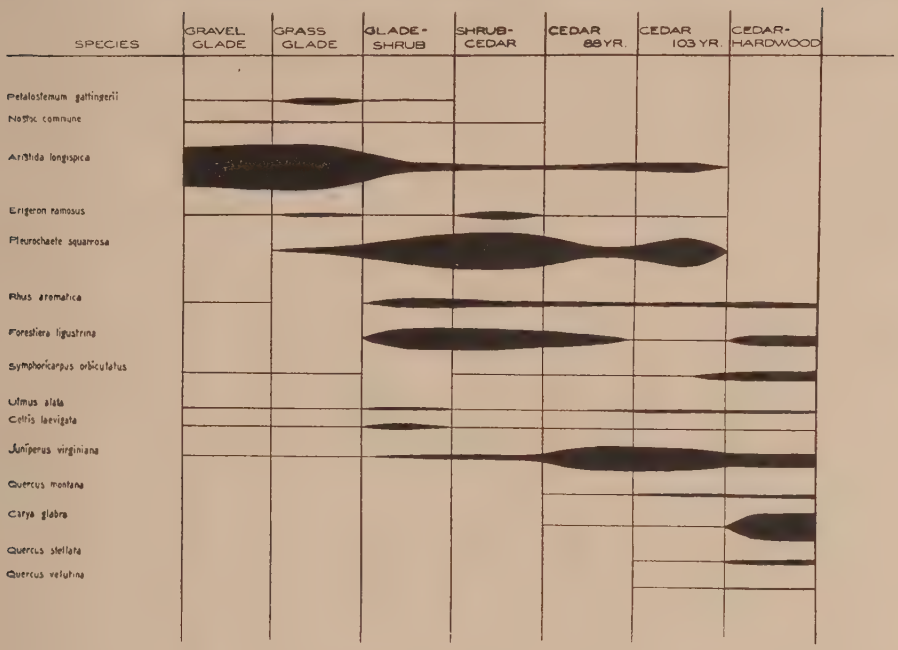

FIG. 14. Dynamic behavior of species through series of glade communities. Thickness of line represents importance of species.

sistently higher than those of other species. The sub-dominant position and fairly regular occurrence of *Ulmus alata* and *Celtis laevigata* in glade woods is indicated by the phytographs of those species.

The gradual increase with age of stand in number of size classes represented and in the density and frequency of the oaks and hickories is shown graphically here. All three species reach the overstory in the cedar-hardwood stand, with enough reproduction to suggest continued competition with the cedars.

Cover-stratification diagrams (fig. 13) show general profiles of communities. Height and coverage of each layer is indicated, as well as number of species.

Importance of the cryptogam layer increases through the shrub-cedar stage, but shows an unexpected reduction in the 88-year stand. This was a thin stand with extreme hyperdispersion of cryptogam species. The decline from 103-year cedar to cedar-hardwood would be expected on the basis of comparison with mature hardwood stands in which cryptogams are frequently negligible.

The herb layer reaches one peak in grass glades where it is the dominant stratum, and another lesser one in the shrub-cedar stand. Its coverage is of minor importance in the forest stands.

Shrubs reach a 50 per cent coverage in glade-shrub and shrub-cedar stands, but drop back to the 25 per cent cover class in both cedar stands. This is probably because of mortality of shrubs that fail to survive competition with the trees. A second peak is reached in the cedar-hardwood stand, where spreading *Symphoricarpus* and hardwood seedlings make a considerable increase in the shrub layer.

Trees over 10 feet high were not present in open glades but reached the 25 per cent coverage class in the glade-shrub stand. Increase in height of tree layer is indicated in the shrub-cedar diagram and further increase to full height shows on the cedar woods diagrams. Coverage in these forest stands does not exceed 50 per

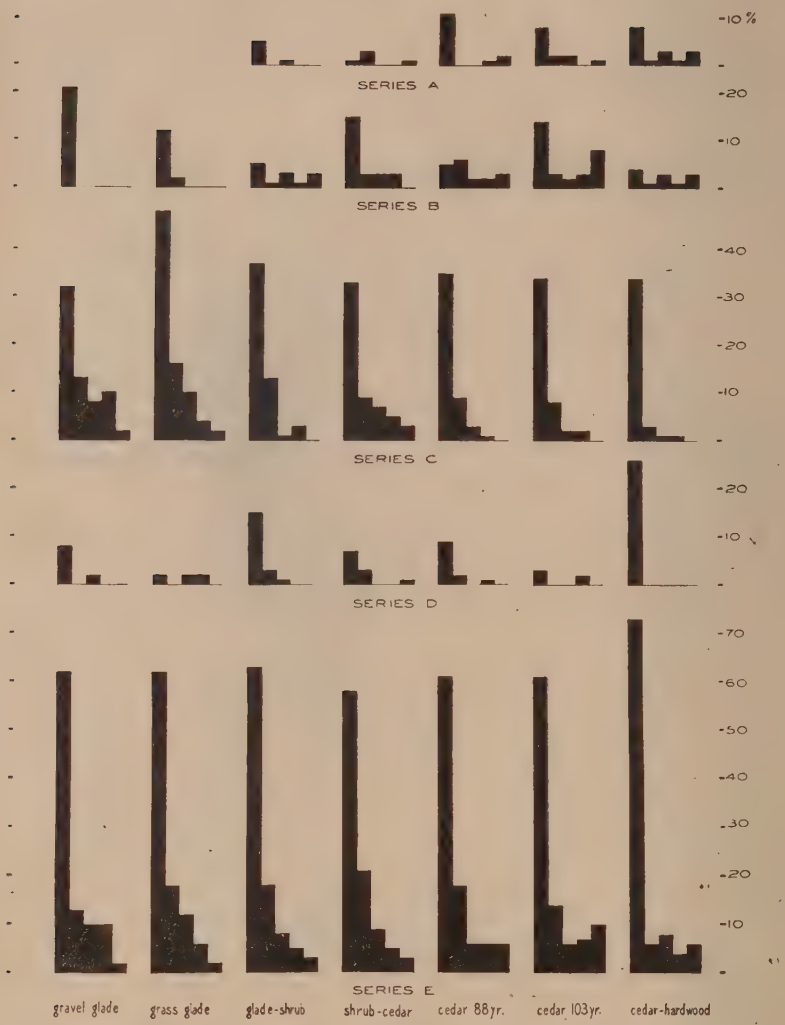

FIG. 15. Frequency diagrams of glade and glade woods communities. Series A—tree layer; series B—shrub layer; series C—herb layer; series D—cryptogam layer; series E—total.

cent in either case. This situation is explained by the spacing of individual trees because of the origin of such woods as lines of trees interspersed with glades. Addition of hardwoods is enough to result in increasing coverage to 75 per cent in the cedar-hardwood forest.

Linkage of these communities by the gradual replacement of a few dominants at a time is illustrated in figure 14. The communities show an obvious relationship which appears to be successional.

Frequency diagrams (fig. 15, series E) of each community investigated show an abnormally high peak in class A as compared with class E, which shows little or no increase. The three forest communities have a more nearly normal curve than the glade and glade-shrub communities. Examination of frequency diagrams of the

various layers shows that the leveling or slight peak in class E of forest communities is caused by the frequencies of shrubs and trees. Through all the communities the abnormal class A is most conspicuous in the herb and cryptogam layers, several of which have no class E at all. The hyperdispersion of glade species, especially herbs and cryptogams, is strikingly illustrated by these diagrams.

Soil: Soil from the rocky cedar woods was highly organic, as shown by the loss on ignition, 28.3 per cent. Pore space was fairly high and volume-weight low. Capillary capacity was high (101 per cent) and so was wilting percentage (20.5 per cent). A great deal of moisture was available during most of the spring but after ten days of drought was reduced to 0.3 per cent of the dry weight of the soil.

Wilting percentages of open glades (9.1 per cent) and glade wood soils (11.1 per cent) were in general lower than that of the organic soil; the capillary capacity was correspondingly lower and the range of moisture available through the growing season was considerably less than in the rocky stand. Less humus was present and pore space was quite variable. Volume-weights were slightly greater than in the organic soil. Soil was increasingly deeper through the successional stages illustrated by these samples.

Discussion

Cedar glades existed in Middle Tennessee probably long before settlement by the white man. The earliest botanical descriptions of the area mention a glade flora including the same species that are present there today. One expects extremely slow change in vegetation when its development must wait for rock to weather into soil. This has been true in the glades—it is even likely that lumbering has increased the acreage of open glades in the last 200 years rather than that succession has reduced it by proceeding steadily toward the climax.

Algae have been found to be important constituents of the pioneer stages of succession in several xeric habitats other than glades. Booth ('41) found that Cyanophyceae, including *Scytonema* sp. and *Nostoc commune,* constitute an initial stage of succession on eroded lands in the southwest. *Oscillatoria* and *Nostoc* are among the algae thriving in the rain-crust of desert soils (Fletcher and Martin, '48). Fritsch ('27) considered the Cyanophyceae the dominant algae on rock surfaces and algal growth the first stage of succession on chalk. Although not mentioned in regard to succession, *Nostoc terrestris* is present in Missouri glades (Erickson, Brenner and Wraight, '42) in much the same habitat as *Nostoc commune* occupies in glades in Tennessee.

Among the lichens only foliose forms seem of any importance in initial stages in Tennessee glades. They, like *Nostoc commune,* have the ability to withstand conditions of extreme dryness on the surface of the rock and to revive quickly into gelatinous masses when wet. These masses must add some humus to the soil of young mats.

The importance of shade in determining the trend of bryophyte succession on rock is evident from the very beginning of colonization. *Orthotrichum strangulatum* is the important pioneer in partial shade and grows directly upon the rock. It does not colonize unshaded rock nor play any part in the early stages of development there. No bryophyte except *Pleurochaete squarrosa* is important in both sun and shade, and it enters sunny situations only after herbs that furnish some shade are present. Planting of *Pleurochaete* fragments from a six months old herbarium specimen produced new plants by budding of old stems and by regeneration of protonema from leaves. The protonema produced growing shoots of *Pleurochaete.* Regeneration after six months of storage in a steam-heated laboratory is fairly conclusive evidence that its absence from exposed rock is not due to its inability to endure desiccation, and so must be related to temperature or radiant energy as such. An entirely different

group of mosses and herbs occurs under shade than in the open. Slightly better moisture conditions prevail in the shade during the wet season, however, and tests of each species would be required to discover which are limited by light and which by water.

Two stages in glade development may be considered sub-climaxes, the duration of which depends primarily upon rapidity of soil formation and maturation. The open glade stages exist as such for a period of time determined by the extent of soil formation and degree of disturbance by man. Scraping of open glades for gravel is common practice throughout the region and tends to hold them in an open condition. Secondary succession following scraping is simply a repetition of herb-grass vegetation, so the pattern of succession is not changed, development is merely delayed by numerous repetitions of the same stages.

The second possible sub-climax is the red cedar stand established in crevices of rock with expanses of flat-topped blocks of limestone between trees. This kind of stand probably lasts for an indefinite period, even if undisturbed. The scarcity of soil precludes the entrance of mesophytic tree species. Such cedar stands remain fairly open until weathering widens the crevices sufficiently to permit a closed stand to develop. When that occurs, the light-requiring cedar (Steyermark, '40) may be replaced by hickories and oaks. This does not mean that the stand proceeds directly to the mixed mesophytic climax, but it does foreshadow the end of the red cedar sub-climax and its probable eventual replacement by an oak-hickory pre-climax such as exists in other dry parts of the Basin.

That open glade associes are replaced by shrubs and trees is evidenced by the spreading of shrubs into grass glades and the growth of individual trees in the open. The presence of old cedars well covered with limbs from base to top and surrounded by younger clear-trunked trees is evidence that such trees developed in the open (Griggs, '34) and have since been surrounded with forest. Linkage of associes by gradual replacement of dominants also indicates the successional relationships of the associes.

Cutting of cedar is a factor in maintaining cedar stands on soil. Usually cutting opens the stand and exposes seedlings and transgressives to much higher light intensity than before. The less light tolerant species may thus be eliminated, and the stand may come back to red cedar.

On thin soil, erosion frequently follows cutting and rapidly sets the area back to early if not initial stages of succession. Some areas are washed so bare of soil after cutting that the algae-bryophyte pioneers enter and the long slow process begins again.

In a few instances, where there were young hickories 12 to 18 feet tall forming an understory in cedar woods, cutting of cedars left a fairly dense growth of hickory. Such stands must surely result in hickory consociations sooner than if left in competition with cedars.

Scraping of gravel and early cutting of cedars will undoubtedly maintain open glade and glade woods sub-climaxes longer than would be the case in the normal course of events, but cutting an overstory of cedar leaving a well-established understory of hardwoods must hasten development of later stages.

Comparing soil data from stations representing various stages of succession from open glade to woods, one finds a correlation with only two sets of figures, those of depth of soil and available moisture taken at the end of a ten-day drought. Each succeeding stage is on deeper soil than the preceding. After 10 days of drought, moisture in the mat on the rock, the open glade and a tongue of woods separating two glades was well below the wilting percentage of those soils. In cedar and cedar-hardwood stands, moisture conditions were safely above the wilting percentage. No consistent corre-

lation of amount of available water with developmental stage was apparent from a study of moisture conditions during the wet spring growing season. This suggests that when water is plentiful it is plentiful in all locations, but when it becomes a limiting factor, conditions are more extreme earlier and therefore longer in the shallower soils. Freeman ('33) found the moisture in shallow soil of open glades to be frequently below the wilting coefficient during spring, summer and fall; less frequently so in cedar woods and only once in the upper six inches of soil in an adjoining hardwood stand.

Conclusions

1. Vegetation that develops in closely placed cracks in glade rock results in a cedar sub-climax that is maintained until the interjacent rock disintegrates and sufficient soil is provided for survival of mesophytic species. Shade of such a stand influences the succession of bryophytes that occur on rock within it.

2. Primary succession beginning on sunny rock and leading to open glades and woods on soil indicates steady, if slow, progression toward the mixed mesophytic climax.

3. Artificial disturbances (lumbering, scraping, grazing, erosion) result in maintaining medial stages of development for long periods of time and in setting areas back to earlier stages. Secondary succession following such disturbances is similar to primary.

Exception to this general statement must be made for cutting an overstory of cedar from a stand with a well-established understory of hardwood, in which case the hardwood is released from competition with cedar and develops more rapidly than normal.

4. Succession of associes is correlated with depth of soil which in turn determines the rapidity with which the permanent wilting percentage of the soil is reached.

5. The fact that glade communities develop into hardwood stands similar to others in the region not on glade soil, substantiates the conclusion in a previous paper (Quarterman, '50) that mineral content of the soil is not a primary factor in the controlling effect of glade rock upon vegetation.

Summary

Two general lines of vegetational development occur in cedar glades in Middle Tennessee. They are determined by position and size of crevices in the rock and each results in cedar woods. One of these begins in direct sunlight with the accumulation of a little soil on the rock and the growth of Cyanophyceae, chiefly *Nostoc commune,* upon it. This is succeeded by *Grimmia apocarpa,* the presence of which anchors the soil and adds organic matter to it. The *Grimmia* stage is followed, in the deeper parts of the mat, by a *Petalostemum-Erigeron-Pleurochaete* stage, which is succeeded by shrubs and trees if these woody plants find a deep enough foothold in the rock to survive. Mats may spread, coalesce and become open glade communities.

The second line of development begins with establishment of vegetation in cracks in the rock. The first plants there are herbs, which are followed by shrubs and trees. If cracks are widely spaced, gravel and soil accumulate on the surface of the rock between them, and further development results in open glades separated by lines of trees and shrubs. In this case, the thin gravelly soil is usually covered first with *Petalostemum, Aristida* and *Sporobolus.* As soil and vegetation develop, *Sporobolus, Aristida* and other grasses become dominant and persist for a long time as a grass stage interspersed with herbs. When invaded, this stage is replaced by a *Forestiera-Rhus aromatica-Symphoricarpus* thicket in which cedar, winged elm and hackberry become established. These trees grow into an open

stand and eventually may be replaced by hickories and oaks.

If the cracks are close together, and the vegetation in them proceeds to the tree stage a different type of bryophyte succession occurs on the shaded rock between. *Orthotrichum strangulatum* initiates succession. It is replaced by *Pleurochaete squarrosa* which is invaded by *Entodon, Thuidium* and *Climacium. Aquilegia* and various ferns grow on these moss mats but tree seedlings survive only in cracks that are filled with soil. These are sub-climax cedar stands that endure until enough soil accumulates to support growth of mesophytic species. Shade is the important factor in determining the course of bryophyte succession in such a stand.

Depth of soil and rapidity of water loss as conditions become extreme are correlated with the developmental condition of the stands. No correlation of data concerning wilting percentage, water-holding capacity, volume-weight or amount of organic matter could be made with successional development of vegetation.

Soil on shaded flat rock in a sub-climax stand was highly organic with high water-holding capacity and high wilting percentage. These soils had a greater range of available moisture through the growing season than the clay soils from open glades and glade woods, but reached the wilting percentage almost as quickly when conditions became extreme.

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THE RELATION OF COPULATION TO FECUNDITY AND POPULATION GROWTH IN *DROSOPHILA MELANOGASTER*[1]

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Introduction

The role of males in the growth of a population has been well demonstrated by Park ('33) and MacLagan ('32) with *Tribolium confusum*. They showed that the fecundity of Tribolium at densities below the optimum is submaximal because the females do not experience repeated copulation. This point was tested further by Crombie ('43) who showed that with well-copulated females there was no fall in fecundity afterward at low densities. In Drosophila, it also has been reported that mating is a stimulation to egg laying, the effect being to alter both time and rate of egg-laying. Guyenot ('13) found in *Drosophila ampelophila* (= *melanogaster*) that copulation stimulated almost immediate oviposition; in fact, egg deposition occurred so soon that some of the eggs were not fertilized. Shapiro ('32) reported that virgin females started to lay eggs on the seventh day after emergence, while the mated females started on the second day. Hanson and Ferris ('29) reported that mated females laid an average of 50 to 100 per cent more eggs than unmated ones, and that this increase in egg production occurred even when the females were mated to sterile males. However, as Shapiro mentioned, some unmated females may lay more eggs than some mated individuals.

In an intensive study on the population growth of *Drosophila melanogaster* in cultures, the relation of male flies to fecundity and fertility of the female flies was investigated. It was thought that inasmuch as there may be different numbers of males and females in a culture and since they may be of different ages, the significance of some of the male-female relationships should be known before the population growth as a whole could be analyzed.

The flies were reared with the technique described by Hodson and Chiang ('48) except that cylinders 17 mm. in diameter and 45 mm. long were used in place of the larger cylinders. Flies of both sexes were introduced into the cylinders in various numbers and at various times as they were required. Fecundity, represented by the number of eggs laid, was checked daily. Optimum conditions were also set up for egg hatching by placing the oviposition blotter in a Petri dish with a few drops of water. The numbers of eggs hatched were checked on the following day. Since the conditions were favorable for egg viability, the number of eggs hatched was considered to represent the degree of fertility.

Different Sex Ratios

The sex ratio of the progeny of paired matings has been reported as about 1 to 1 (Laurinat, '31). However, under crowded larval feeding conditions, it was shown by L'Heritier and Teissier ('33) that the males constitute only one-third of the total emergence. They explained this ratio by a higher tolerance of the female larvae to high densities and to a low food supply. Bonnier ('26) demonstrated that male pupae take 4 and 10 hours longer to develop than female pupae at 25° and 30° C. respectively, and Eloff ('40) presented data showing the same phenomenon. It is also known that males have a shorter normal life than the females (Alpatov and Pearl, '29). All these findings point to the possibility of there being a lower percentage of males than females in a stand-

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ing population either in the field or in culture.

These facts led to the question of how fertility and fecundity would hold up with a low percentage of males. Experiments were run with female-male ratios of 10/1, 5/1, 1/5, and 1/10. The fecundity in the first three cases was the same as if the sex ratio had been 1/1. For the last ratio, however, the fecundity was lower than in the others. This may have been due to the disturbance caused by a large number of males attempting to mate with a single female. The fertility of all the series ran close to that of paired females. This finding was to be expected because of the high rate of mating activity shown by the males. Duncan ('30) observed that in one case a single male mated with 14 virgin females in one day, and that a vigorous male was able to fertilize about 14,000 eggs, the number that ten females will lay in their lifetime. Demerec and Kaufmann ('41) noted males mating with nine to ten females in a day's time, while Hyde ('24) also recorded more than ten females were mated by a single male and produced fertile eggs. From these findings it is apparent that a low percentage of males in a population will not be an important factor affecting either fecundity or fertility, at least in a small restricted habitat.

Isolated Gravid Females

In a population started from a single pair of adults of the same age, there is chance for either one of them to die in a short time. When the male dies before the emergence of a new generation, the ability of the female to keep laying fertile eggs will be an important determinant in shaping the further growth of the population. This characteristic would be just as important in the establishment of new populations in the field when a single gravid female has become isolated from other Drosophila. Experiments were set up to determine how the fecundity and fertility would change when the female had been associated with a male for a certain period of time and then was isolated. Increasing periods of one to seven days were used as exposure time. Table I shows the total oviposition, the total hatching, the total number of days with fertile eggs and the number of days with

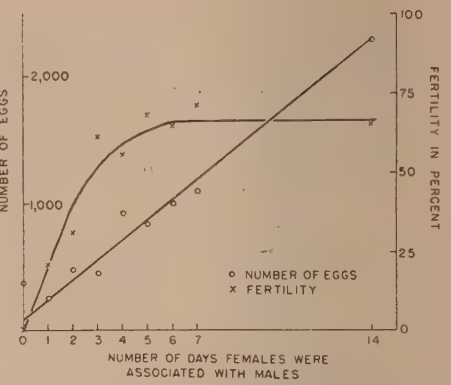

Fig. 1. Fecundity and fertility of Drosophila females associated with males for different periods of time.

Table I. *Fecundity and fertility of Drosophila females associated with males for different periods of time*

Number of days females were associated with males	0	1	2	3	4	5	6	7	14	23
Number of tests	3	5	5	4	2	3	4	3	1	1
Average number of eggs laid per female	33	252	488	453	886	857	1006	1107	2313	2621
Average number of eggs hatched	0	15	48	144	308	316	451	591	1220	2369
Percentage of fertility	0	20	31	61	56	68	64	72	65	93
Longevity in days	36	37	40	41	44	44	41	41	55	30
Days with fertile eggs	0	5	8	12	11	13	14	17	25	25
Average number of days with fertile eggs after removal of males	0	4	6	9	7	8	8	10	11	—

fertile eggs after the male was removed. Data for a series of tests with virgin females and females whose mates died on the 14th and 23rd days are included also for comparison. The results are illustrated in figures 1 and 2.

Several points of interest are brought out by this study. The total egg laying increased with an increase in the length of the time that the female was associated with males, showing an almost straight line relationship. In addition, fertility increased with an increase in the length of the time that the female was associated with males up to a period of seven days. A further increase in contact time had little effect on fertility. This is comparable to the findings of Park ('33) in Tribolium where copulation in excess of a certain amount had no further effect upon fertility. Finally, the number of days during which fertile eggs were produced after the removal of the male increased slowly with an increase in the length of the time that the female was associated with males, the longest time on the average being about 10–11 days, regardless of how long the female stayed with males.

It is clear, then, that there is a period of about ten days in which a female can lay fertile eggs without the male, if this female has been associated with males for more than seven days. With a briefer contact period with males, however, this time period is shorter. It has been shown also by Kaufmann and Demerec ('42) that Swedish-b flies can lay fertile eggs for ten days after the last copulation. The ecological implication of this characteristic is the fact that the females, when isolated from males, can reproduce successfully for a period of time long enough for another generation to emerge at an average temperature of about 25° C. Longevity, in those cases where it was observed, was not affected by the amount of egg laying. This seems not in accordance with the findings of Alpatov ('32) and Gowen and Johnson ('46). It may be explained on the basis that the lowering of fecundity due to a lack of mating does not play the same role as difference in genetic constitution with which these authors dealt.

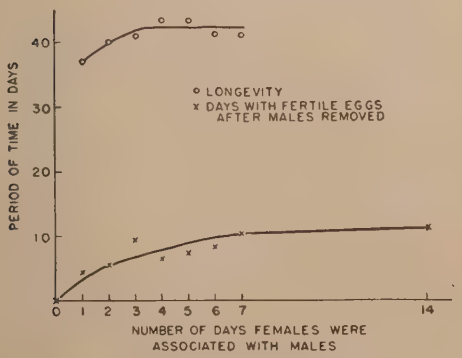
PERIOD OF TIME IN DAYS
40
30
20
10
o LONGEVITY
x DAYS WITH FERTILE EGGS AFTER MALES REMOVED
0 1 2 3 4 5 6 7 14
NUMBER OF DAYS FEMALES WERE ASSOCIATED WITH MALES

FIG. 2. Longevity and the period with fertile eggs after the removal of males for females associated with these males for different periods of time.

FEMALES MATED AT DIFFERENT AGES

Since the normal adult life is several times longer than the pre-imaginal development, the co-existence of adults of more than one generation and that of adults of different age classes in a population is the usual condition. Laurinat ('31) made a study on the mating of pairs of increasing ages. He found that the sex-ratio of the progeny was always 1 to 1. The productivity of males of different ages has been studied by Duncan ('30), and was shown to be highest for the first 5 days with an almost regular decline to 30 days. At this time it declined sharply. The total number of eggs fertilized by males mated from the second day of life was found to be above 10,000, and eggs fertilized by males mated from the 34th day or later was not more than 8,000. No reference was found as to the effect of female age on both fecundity and fertility, so experiments were conducted to determine this point.

Virgin females were reared singly in oviposition cylinders. Every five days virgin males were introduced into some of the cylinders, one in each. In this way, pairs of virgin males and females of dif-

TABLE II. *Average daily fecundity and fertility of Drosophila females of different ages mated with virgin males*

Sequence of time in 5-day intervals	Day of male introduction					No male (virgin female)
	1st	6th	11th	16th	21st**	
Average daily fecundity						
1–5	42*	4	1	2	1	3
6–10	58	69*	11	12	9	1
11–15	56	61	37*	12	17	5
16–20	53	30	44	36*	24	12
21–25	48	37	32	30	38*	13
26–30	42	18	33	14	35	11
31–35	39	2		13	25	10
36–40					15	10
Average fertility in per cent						
1–5	91*	0	0	0	0	0
6–10	95	92*	0	0	0	0
11–15	92	86	85*	0	0	0
16–20	98	82	95	90*	0	0
21–25	88	64	97	91	44*	0
26–30	27	45	96	75	48	0
31–35	0	0		77	17	0
36–40					0	0

* Males introduced.
** Two replicates only, others have three replicates.

ferent ages were combined at 5-day intervals. The oviposition surface was renewed and eggs were counted each day both before and after the introduction of males. The average daily oviposition and the average viability of eggs over the 5-day periods are summarized in table II, and illustrated in figure 3. A series of virgin females was also included in the experiment.

As shown by other workers, fecundity of Drosophila varied with age, generally reaching a peak on the sixth to tenth days of female life and then gradually dropping off. It is shown here that the same change occurred also with virgin females, although the peak was much lower and was reached at a later time. A sudden increase in fecundity following the introduction of males was conspicuous in every case, but the falling off of fecundity afterward was faster in females mated at an older age than in those mated at a younger age. It was also shown that the fertility of females mated from the first day of their life was 80 to 100 per cent in contrast to only 40 to 60 per cent for those mated at an older age. These data indicate that females of different ages responded to the stimulating effect of mating to about the same extent, but the chance of fertilization taking place decreased with age. Why fertility at a corresponding age should be lower when the female has not mated previously is not understood.

SUMMARY

Female-male ratios of 10/1, 5/1 and 1/5 gave the same fecundity as that of 1/1. A ratio of 1/10, however, gave a fecundity lower than the others. In the experiments on isolated gravid females, it was shown that the total egg laying increased with an increase in the length of the time that the female was associated with males, while fertility increased with an increase in the length of the time that the female was associated with males up to a period of seven days. A further in-

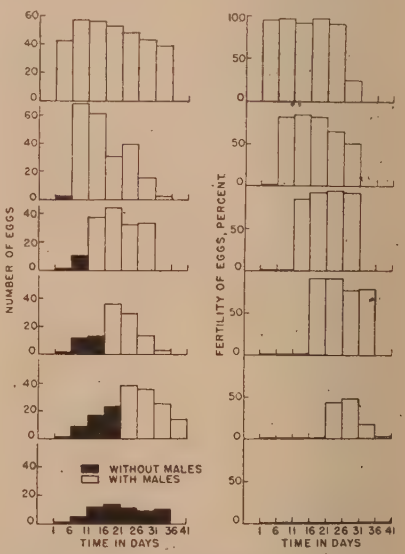

FIG. 3. Changes in fecundity and fertility of Drosophila females of different ages mated with virgin males.

crease in the latter had little effect on fertility. Finally, the number of days during which fertile eggs were produced after the removal of the male increased slowly with an increase in the length of time that the female was associated with males, the longest time on the average being about ten days regardless of how long the female stayed with males. Experiments on females mated at different ages showed that the sudden increase in fecundity following the introduction of males was conspicuous regardless of female age at the time of introduction. Females of different ages responded to the stimulating effect of mating to about the same extent, but the chance of fertilization taking place decreased with age. The biological characteristics demonstrated here make it unlikely that the growth of populations of Drosophila would be affected appreciably by a temporary absence of males, a low percentage of males, or a difference in male and female ages.

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AN ECOLOGICAL RECONNAISSANCE IN THE NATIVE HOME OF *METASEQUOIA GLYPTOSTROBOIDES*

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INTRODUCTION

The recent discovery of *Metasequoia glyptostroboides* Hu and Cheng, a contemporary species of a genus recognized on the basis of fossil materials only a few years before, has aroused widespread interest. Many brief papers have appeared, but almost nothing has been reported concerning the ecology of the species—its relations to its physical environment and to its plant associates. The only treatment of this phase—very brief and general—is by Chaney ('48a), whose interest in the paleoecology of the Cretaceous and Tertiary led him to make observations upon the environment and associates of Metasequoia, modern representative of an ancient genus, on the occasion of his visit to its native home early in 1948. The findings presented in this paper agree with and amplify his observations.

In the summer of 1948 a welcome opportunity came to the senior author to join an expedition to the native home of Metasequoia. The leader was Dr. Wan-chun Cheng of National Central University, Nanking. Dr. Cheng and Dr. Hsen-hsu Hu, of the Fan Memorial Institute of Biology, Peiping, are the men to whom credit must be given for organizing the field work dealing with Metasequoia during the years 1946 to 1948 and for determining the taxonomic status of the species. The senior author's share in the activities of the expedition was to gather as much information as possible bearing upon the ecology of Metasequoia—its physical environment, its ecological life history, and its community relations. Due to the large proportion of the total time consumed in travel to and from the region, the volume of results is less than had been hoped. It is a matter of regret, in particular, that work had to be limited to the immediate environment and closely associated vegetation; there was no time available for a general survey of the vegetation of the area. In view of the almost complete previous lack of knowledge concerning the ecology of Metasequoia, the present study, limited as it is, surely has value, and it will serve as a foundation for future investigations. The junior author's share in the project has been the addition of materials from the literature not available in China, formulation of certain conclusions based upon the facts discovered, and final organization of the manuscript for publication.

Dr. Cheng's expedition of 1948, planned under the auspices of the Department of Forestry of National Central University, was supported in the main by a grant from the American Philosophical Society under the joint sponsorship of Dr. E. D. Merrill of the Arnold Arboretum and Dr. R. W. Chaney of the University of California. The senior author's field expenses were defrayed by a grant from the Graduate School of the University of Minnesota, to which grateful acknowledgment is made. The authors wish to express their sincere appreciation to the following persons who materially aided in the study: Professor S. S. Chien, eminent Chinese botanist, for his kindness in reading and correcting the original manuscript; Dr. W. C. Cheng, for identification of plants and for valuable suggestions;

Mr. C. T. Hwa, one of the members of the expedition, for assistance in various ways; Miss C. Y. Chien, for her generous help in preparation of the maps; Dr. J. R. Borchert, for assistance in locating climatic data; Dr. E. D. Merrill and Dr. R. W. Chaney, for reading and criticizing the manuscript in its final form, checking plant names and bibliographic references, and for their generous cooperation in all phases of the project.

Previous Work

The first specimens of Metasequoia were collected in 1944 [1] by Mr. Tsang Wang of the Central Bureau of Forest Research, who assumed them to be *Glyptostrobus pensilis* (Stount.) K. Koch. In 1945 Mr. C. L. Wu, of the Department of Forestry of National Central University, while working in the herbarium of the Central Bureau of Forest Research, found these specimens and realized that they were not Glyptostrobus but something absolutely unknown. Dr. W. C. Cheng, upon examining the specimens, agreed with his conclusion. In 1946 more complete collections were obtained, and Dr. Cheng referred them to Dr. H. H. Hu of the Fan Memorial Institute of Biology in Peiping. Dr. Hu recognized the tree as belonging to the genus Metasequoia, which had been described by Miki ('41) on the basis of fossil material from Japan and Korea. Hu and Cheng later ('48) published a description of the living species, *Metasequoia glyptostroboides*.

In the appended bibliography an attempt has been made to assemble all the publications that have appeared dealing with the living species of Metasequoia.[2] There are doubtless omissions, but quite certainly none of scientific importance.

In the short space of three years (1947–1949) about 50 publications have appeared dealing with Metasequoia, almost all of them in China and the United States, and about equally divided between scientific contributions and more or less popular articles. Among the scientific contributors, the following have dealt with taxonomic and phytogeographic matters: Chaney ('48a), Haas ('49), H. H. Hu ('46, '47), Hu and Cheng ('48), Merrill ('48a, '48b), Merrill and Chaney ('49), Schopf ('48b), Sze ('48d). The following publications are concerned with the plant itself—its morphology, anatomy, growth, cytology: P. C. Cheng,[3] Creech ('48), Day ('49), Ingram ('48), Kan, Hao, and Hwa ('48), Li ('48a, b), Liang, Chow, and Au ('48), Morley ('48), Skinner ('49), Stebbins ('48), Sterling ('49), Yu ('48). The paleobotanical aspects are treated in the following: Andrews ('48), Chaney ('48a, '48b, '48c, '49a, '49b), Hu ('46), Hu and Cheng ('48), Merrill ('48a, '48b, '48c), Merrill and Chaney ('49).

Location, and Route of Expedition

Shui-hsa-pa,[4] the objective point of the expedition, is an unimportant settlement, to be found neither in atlases nor on the district map, in Li-chuan-hsien (Li-chuan district), Hupeh province, close to the border of Szechuan (figs. 1, 2). The approximate latitude is 30° 10′ N, longitude 108° 35′ E. It is about half way between the Pacific coast on the east and the Tibetan Plateau on the west, and between the Gobi Desert on the north and the China Sea on the south. It lies

[1] This date cannot be absolutely verified from sources presently available. It may possibly have been a year or two earlier.

[2] Special acknowledgment is due Dr. E. D. Merrill for his assistance in compiling this bibliography.

[3] Unpublished manuscript, "Leaf anatomy of Metasequoia," Nat. Central Univ., Nanking. 1948.

[4] Shui-hsa-pa means "Place of the Water Pine," an obvious reference to Metasequoia; Shui-hsa has also been translated as water larch. As to English spelling of Chinese place names (and hyphenation and capitalization as well) there is no standard usage. In this paper the best available authorities have been followed. For the local names, to be found on no map, an attempt at transliteration is all that is possible.

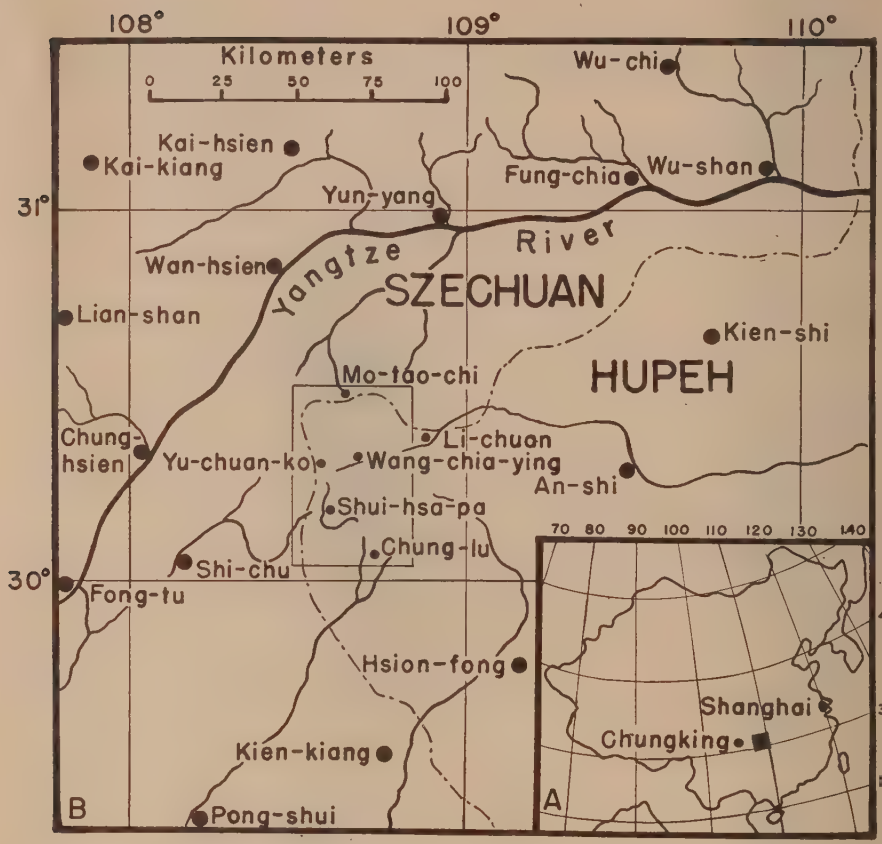

FIG. 1. A. Map of China showing location of B (black square). B. Region surrounding the native home of Metasequoia, with area of fig. 2 indicated. Adapted from Hu and Cheng ('48: pl. 2).

in a flat-floored valley surrounded by mountains, which in this paper will be designated Shui-hsa valley (Shui-hsa-chi). These mountains effectively isolate Shui-hsa-pa from neighboring larger settlements such as Wang-chia-ying and Chung-lu. Access to it is easiest from the latter place, but even here a 500-meter-high mountain range must be crossed.

The route of the expedition was by commercial transportation to Wan-hsien, a large city of eastern Szechuan on the Yangtze, and from there southward on foot to Shui-hsa-pa. The airline distance from Wan-hsien to Shui-hsa-pa is about 80 km; the actual route traveled was 200 km. The longest single day's walk was 65 km. The route lay from Wan-hsien (altitude 180 m), through Mo-tao-chi (1250 m), across the range Chi-yao-shan (1500 m), through Wang-chia-ying (1000 m), across Fu-pao-shan (1400 m), to Shui-hsa-pa (1050 m). The party arrived at Shui-hsa-pa August 23 and left September 20.

TOPOGRAPHY

The general region within which lies the home of Metasequoia is a mountainous table land cut by deep valleys, southeast of the Yangtze River in its local course. The streams flow outward in all directions, but all finally reach the Yangtze.

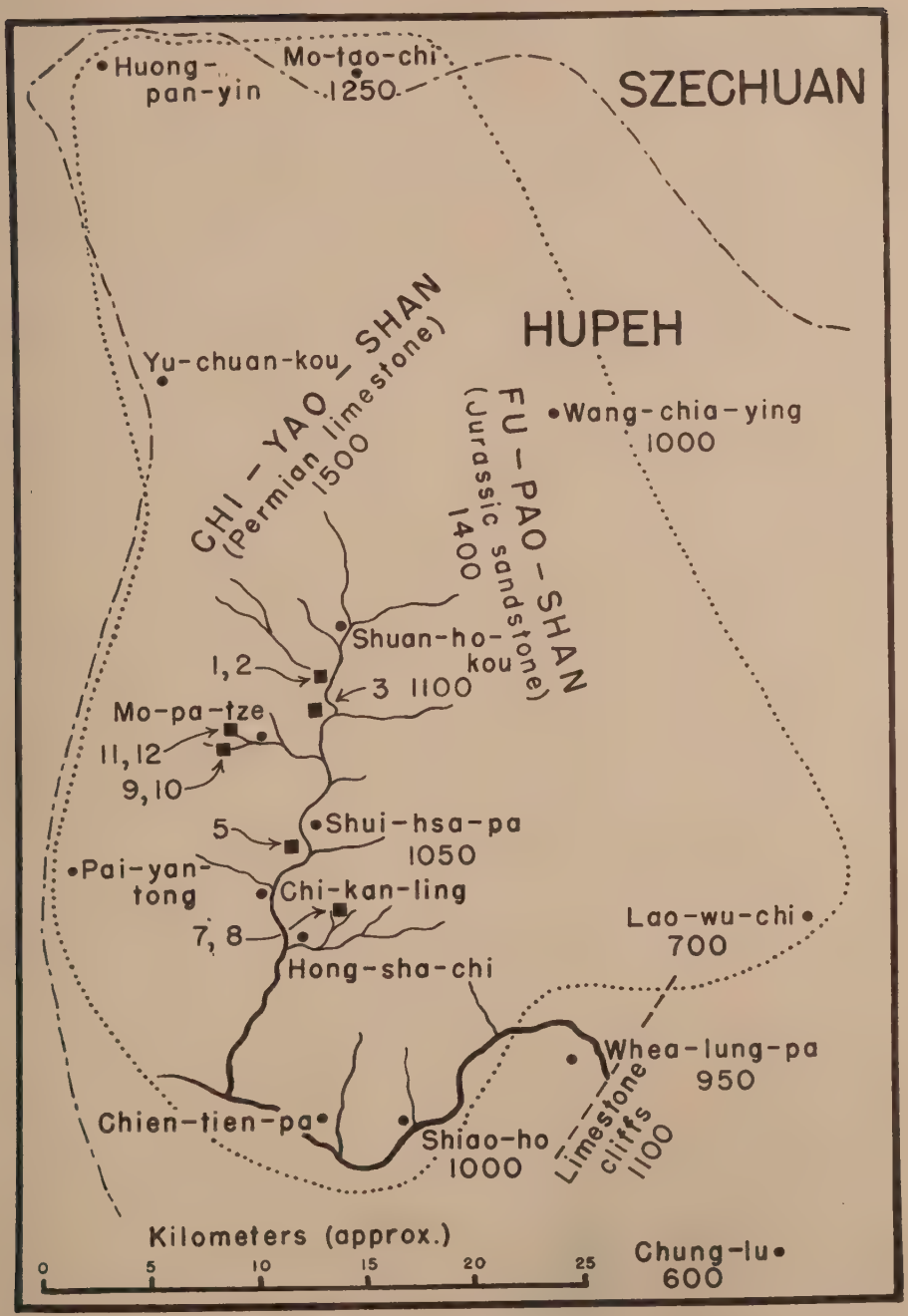

FIG. 2. Sketch map of Shui-hsa valley and its immediate surroundings. Location of quadrats (numbered squares); approximate limits of Metasequoia (dotted line). Approximate altitudes in meters. Shan = mountain range.

The most prominent topographic feature is the mountain range known as Chi-yao-shan, of Permiam limestone, which reaches an altitude of 1500 m above sea level (fig. 2).

Shui-hsa valley, a remarkable closed depression, lies about 60 km southwest of the Yangtze River at its closest point. It is bounded on the west by the Chi-yao-shan and its headwaters are largely in that range. On the east is a roughly parallel range of Jurassic sandstone, Fu-pao-shan, which attains an altitude of 1400 m. The main stream in the valley flows mostly on the sandstone. Its course is southward for about 25 km, then roughly eastward in an S-curve for about 20 km to the point where it disappears underground at the foot of limestone cliffs 200 m high. Its subterranean course is 10–20 km long and it emerges in the general region of Chung-lu. Shui-hsa valley is thus unique in being walled in on all sides, even at the lower end. From Shuon-ho-kou near the headwaters (altitude 1100 m) it drops 150 meters in about 45 km to Whei-lung-pa close to its point of disappearance—a gradient of only 3.3 meters per kilometer. Shui-hsa-pa, in the heart of the Metasequoia area, is about 13 km from the headwaters and 30 km from the point where the stream disappears.

The flat valley floor, 300–600 meters wide in the vicinity of Shui-hsa-pa, is occupied almost entirely by rice paddies. The mountain slopes, rising 400 meters above the valley on the west and 300 meters on the east, are cut by ravines and covered by semi-natural vegetation.

The floor of Shui-hsa valley is higher than most of the valleys of the region; the altitude of Wang-chia-ying valley on the north is 900 m, of Lao-wu-chi on the east 700 m, and of Chung-lu on the south 600 m. The soil of Shui-hsa valley, derived mainly from sandstone, is perhaps not particularly fertile. Pai-yan-tong valley, west of Chi-yao-shan, stands higher than Shui-hsa; it is on limestone, has a denser human population, and the soil is presumably more fertile.

Climate

Climatic data applicable to the Metasequoia region are extremely scanty. With regard to its place in the picture of China as a whole, there is something to be gleaned from works by Chinese and American authors. C. C. Chu ('29) proposed a scheme of climatic provinces which has since been modified and elaborated. The most satisfactory of these later treatments is that of Tu ('36). It forms the basis of Biel's discussion ('45: 147–157, with map), which is followed here.

Shui-hsa valley lies within the Western China Type of Tu, in a strip bounded on the east by the main body of the Central China Type, which covers roughly the lower and middle Yangtze valley, and on the west by an outlier of the Central China Type coinciding with the Red Basin of Szechuan. The Western China Type covers an area of high mountains and plateaus. The subtype including Shui-hsa valley (and Kwei-yang, to be mentioned shortly) is the warmest and driest. Precipitation is, however, adequate; in some other portions of the type it is high. Winters are warmer than on the coast at the same latitude, in spite of altitude, probably because of high cloudiness and protection afforded by mountain ranges against cold waves.

Borchert ('47) has recently formulated a new climatic map of China based upon a slightly modified Köppen plan. According to this, the climate of the Metasequoia region is of the type "Caw" (C = mesothermal, a = warmest subdivision of C, w = winter deficiency of precipitation). The monsoon influence shows itself in a pronounced summer maximum. This is brought about, according to Borchert, by "convergence and overrunning of tropical maritime (mT) air along the polar front, as it migrates northward in spring," producing abundant rain, followed by "convergence of two moist air-

masses—tropical maritime and more humid equatorial maritime (mE)—along the equatorial front," producing equally abundant summer rainfall (see Borchert, *op. cit.*, fig. 3, p. 172).

The region lies 400 km south of the boundary between the C and D climates, which in Borchert's scheme is determined by mean January temperature of 32° F; and 250 km south of the southern limit of occasional "steppe years," which indicates that adequate precipitation from year to year is a dependable quantity.

Chaney ('48a) has attempted an estimate of the climate in the home land of Metasequoia through comparison with that of Chungking, 200 km south-southwest. Examination of the maps and data in Biel ('45) indicates that there is another station with records of certain climatic factors that is probably closer in character to Shui-hsa valley than is Chungking. This is Kwei-yang, in Kwei-chow province, lat. 26° 30′ N, long. 106° 38′ E, approximately 450 km south-southwest of Shui-hsa valley. The difference in latitude (3° 40′) is considerable as compared with Chungking, which is less than one degree south of Shui-hsa-pa. The altitude of Kwei-yang, however (1076 m), is almost exactly the same as that of the upper part of Shui-hsa valley, whereas the altitude of Chungking is only 230 m. The region around Kwei-yang, moreover, is upland, while Chungking is in the valley of the Yangtze. According to Tu's scheme, Shui-hsa valley and Kwei-yang lie within the Western China Type, while Chungking is in the western outlier of the Central China Type. In Borchert's adaptation of the Köppen classification all three stations lie within the type "Caw." Climatic records for Kwei-yang and Chungking are presented in table I; the same data appear in graphic form in figure 3.

The precipitation patterns for Kwei-yang and Chungking are very similar. At Kwei-yang, higher in altitude, average annual precipitation is ten per cent more than at Chungking. Both have a pronounced maximum in early summer with an indication of a secondary peak in September, and an equally pronounced winter minimum. Considering amount of precipitation alone, a definite winter dry season is indicated, but reference to the figures for number of days with precipitation

TABLE I. *Climatic data for Kwei-yang and Chungking (from Biel, '45)*

Monthly and annual precipitation, cm

	Yrs. record	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Ann
Kwei-yang	11	2.54	2.79	3.30	7.11	16.76	21.34	21,08	12.19	14.99	10.92	5.08	2.29	120.39
Chungking	43	1.78	2.03	3.81	9.91	14.48	18.29	13.97	12.70	14.73	10.92	4.83	2.03	109.48

Seasonal distribution of precipitation, per cent

	Winter	Spring	Summer	Autumn
Kwei-yang	6	23	45	26
Chungking	5	26	41	28

Number of days with precipitation

	Yrs. record	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Ann
Kwei-yang	11	16.3	16.0	13.0	16.3	19.5	18.9	19.3	14.8	15.6	16.1	13.9	11.2	190.9
Chungking	43	6.4	7.2	9.4	11.7	14.0	14.6	9.4	9.1	13.7	15.7	10.3	7.4	128.9

Seasonal distribution of days with precipitation, per cent

	Winter	Spring	Summer	Autumn
Kwei-yang	23	25	28	24
Chungking	16	27	26	31

Mean temperature (°C), monthly and annual

	Yrs. record	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Ann	Ann rge	Abs max	Abs min
Chungking	44	9.2	9.9	14.3	19.7	23.1	25.9	28.0	29.1	24.4	19.4	14.8	10.2	19.0	19.9	46	−1.7

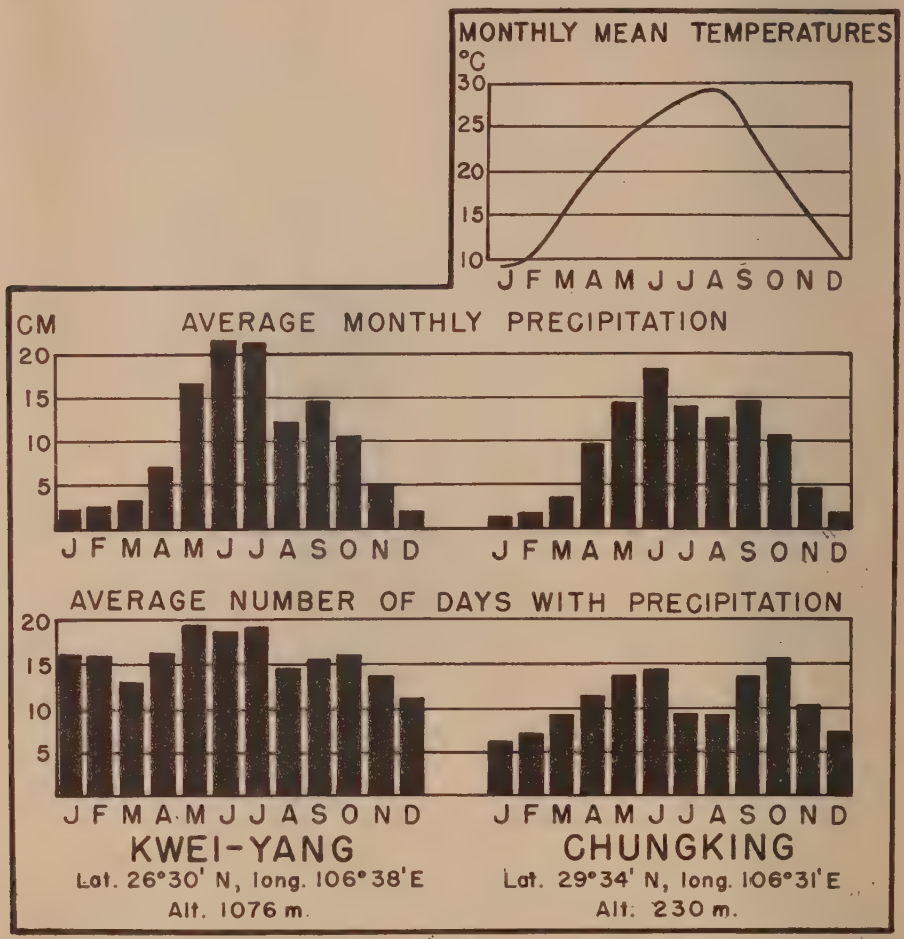

FIG. 3. Graphic presentation of climatic data for Kwei-yang and Chungking.

changes the picture, especially for Kwei-yang. Here, in December, 2.29 cm average precipitation is spread over an average of 11.2 days. For January, 2.54 cm fall in 16.3 days (only three fewer than during the summer maximum of precipitation), and for February 2.79 cm in 16 days. Of the 90 days of the winter months, 43.5 on the average, or nearly half, have precipitation. It is plain that the winter at Kwei-yang cannot be dry; we may fairly assume much cloudiness, high humidity, and frequent slight drizzle. Deficiency in precipitation is compensated by low evapotranspiration.

Since in dealing with such an out-of-the-way locality every scrap of evidence should be utilized, it is worth while to insert here a very brief record of precipitation from Mei-tan, Kweichow province (Nat. Res. Inst. of Meteorology, '44). Mei-tan (lat. 27° 46′ N, long. 107° 27′ E) lies, from Shui-hsa-pa, in the same direction as Kwei-yang, but is 150 km nearer. Its altitude is 770 m. Records for two consecutive years (1941–1942) are available. The summary given below indicates close similarity to Kwei-yang. The even distribution of number of days with precipitation is noteworthy. Total precipi-

tation (average of two years) was 113.5 cm, number of days with precipitation, 165.

	Winter	Spring	Summer	Autumn
Seasonal distribution of precipitation	7%	35%	40%	18%
Seasonal distribution, days with precipitation	24%	25%	26%	25%

It is interesting, though perhaps not significant, to note that with both Metasequoia and Sequoia a season of deficient rainfall is ameliorated by conditions that reduce the rate of transpiration. The seasons with deficit, however, are reversed, and Metasequoia would appear to have an advantage over its relative in that the period of deficit coincides with low temperatures rather than high. At Chungking the winter is definitely drier than at Kwei-yang, though even there, with precipitation occurring on 21 of 90 winter days, a really dry season is not indicated.

As to snowfall in Shui-hsa valley, Chaney ('48a) states that "villagers reported that there is no snow or frost." Mr. C. J. Hsieh, leader of the 1946 and 1947 expeditions, on the other hand, reported that there is some ice and snow in the winter months (Merrill, '48b). At any rate snow, if it occurs, cannot be in great quantity or long-lasting.

Temperature data are available only for Chungking. Winters are very mild and summers hot, the highest temperatures occurring in August, after the peak of precipitation has passed. At Kwei-yang temperatures doubtless range somewhat lower, even though altitude is partially compensated by lower latitude. In Shui-hsa valley temperatures are quite certainly lower than at Chungking, the latitude being approximately the same. Frosts are surely infrequent and light.

In searching for a climatic parallel to this region in North America, the southeastern coastal plain—e.g., Georgia—comes to mind. Temperatures are similar except for lower absolute minima in the American region, and total precipitation is about the same. The seasonal pattern on the coastal plain, however, is markedly different, precipitation being evenly distributed through the year. The same comparison occurred to Chaney ('48a) in drawing a parallel between Metasequoia and Taxodium.

The peculiar topographic situation in Shui-hsa valley may give it a local climate somewhat different from that of the surrounding country. The mountains on east,, north, and west are relatively high and may well afford some protection from the cold, dry air masses that in winter move in from the Gobi Desert to the northwest. The mountains to the south are lower, giving easy access in the summer to the warm, moist air masses from the Pacific Ocean to the southeast.

It is certain that the air within the valley is comparatively stable. Observation shows that while clouds are moving rapidly over the mountain tops there is scarcely any air movement on the valley floor. This stability should operate to keep humidity relatively high and temperatures at a relatively constant level. The daily period of direct sunlight in the valley is shortened due to the surrounding mountains. While the expedition was in the valley the sun rose over the eastern range at about eight o'clock and disappeared behind the western rim about six, giving a period of direct sunlight 4–5 hours shorter than the possible maximum for level land at this latitude. This would to some extent decrease evaporation.

Soils

Data as to the soils of the Metasequoia region are also scanty. Reference to the soil map of China by Thorp ('36) indicates that the area lies within a narrow northwestward extension of the great body of yellowish lateritic soil that covers much of south China. A body of red soils

corresponding with the geographic unit, Red Basin of Szechuan, is close by on the west, and an extensive area of gray-brown forest soil on the east.

Within the area of Metasequoia occurrence, trees of this species have been found only on sandy soils derived from the Jurassic sandstone, and never on calcareous soils derived from the Permian limestones except where planted occasionally by the natives.

Four soil samples were collected from each of the ten 10 x 10 meter quadrats and later submitted to Mr. Y. C. Ma, Director of the Soils Department of the Geological Survey Institute at Nanking. Mr. Ma's report indicates some textural diversity; coarse sandy silt loam, sandy silt, fine sandy silt, loamy silt are mentioned. Differences in texture were found in quadrats close together, and it is assumed that all of these are local variants of an essentially homogeneous type. All samples agree in being slightly acid or circumneutral, the range in pH being from 6.5 to 7.1; and in having little or no available nitrogen. Samples from six of the quadrats showed characteristics suggesting nearness to the gray-brown podzolic soils.

Vegetation

Taxonomically the flora of China is comparatively well known; very little has been done on the vegetational aspects. Various phytogeographic schemes have been presented, which differ greatly. The Metasequoia area falls within the Szechuan-Kweichow Highland Forest Region of Huang ('41), and the Yangtze Forest Region of Teng ('48). Practically nothing is known as to the communities and their successional relations. The senior author reports the following species of trees as being common in the region, in addition to the immediate associates of Metasequoia listed later:

Lithocarpus viridis R. & W.
Quercus glauca Thunb.
Quercus glauca f. *gracilis* R. & W.
Quercus sp.
Michelia sp. cf. *M. floribunda* Finet and Gagneh
Ostrya multinervis Rehd.
Populus tremula L.
Pinus massoniana Lamb.
Schima superba Gardn. and Champ.

The above list and table II indicate in general a mixture of deciduous angiosperm trees and gymnosperms, and this is confirmed by Chaney's observations ('48a). He also reports (personal communication) two large Ginkgo trees growing in Shui-hsa valley, quite certainly planted.

History of Shui-hsa Valley

The senior author was fortunately able to glean something concerning the cultural history of Shui-hsa valley through conversations with Mr. Wu, more than sixty years old, who with his two brothers, prosperous and intelligent men, are descendants of the earliest permanent settlers in the valley. The region was originally controlled by primitive nomadic tribes, some of whom still live in adjacent mountains. Mr. Wu's ancestors migrated from Szechuan to the Shui-hsa-pa region about two hundred years ago. From the Ching tribe in Chung-lu they bought an area of mountain land in the vicinity of Shui-hsa-pa more than eight km long. At that time, according to Mr. Wu, the mountain slopes bore a forest cover so dense that one could not see the blue sky through the canopy, and the level valley floor had never been disturbed by man. Fires were set to destroy the forest, and rice paddies were established. Rice culture since then has extended over practically the whole of the level valley floor, and the forests on the mountain slopes have been largely destroyed because of timber use and charcoal making. The era of agricultural economy, with the destruction of native vegetation that it has entailed, thus goes back about two centuries. It is significant that Shui-hsa valley has suffered less than any other part of the region, and one rea-

FIG. 4. A. The type tree at Mo-tao-chi with its temple. B. Buttressed base of type tree. C. The big tree near Wang-chia-ying, the largest measured. D. Close view of the same.

son for this is doubtless the fact that it is a closed basin, with no easy river route into it.

The Natural Habitat of Metasequoia

The region within which trees of Metasequoia have been found is estimated to have an area of about 800 sq km, with altitudes ranging from 700 to 1350 m. The general area in which the tree appears to be a constituent of a natural forest community and where it is actively reproducing is much smaller. It is situated in Shui-hsa valley and forms a strip along the main river 25 km long and less than 1.5 km wide. The altitude here ranges from 1000 to 1100 m. Outward from this center in all directions Metasequoia decreases in frequency. For a considerable distance—5 km south of Shui-hsa-pa and 35 km north to Mo-tao-chi, with altitudinal range of 900 to 1250 m—many good trees occur and some fine large ones, for example, the type tree at Mo-tao-chi (fig. 4A, B) and a very large one at Wang-chia-ying (figs. 4C, D; 5A). The area marked by occurrence of fairly good or large trees may be regarded as the region of optimum growth. The trees themselves may be relics from a time when the natural community including Metasequoia was more widespread than now. The trees most remote from the center, at the lowest and highest altitudes, are in poor condition.

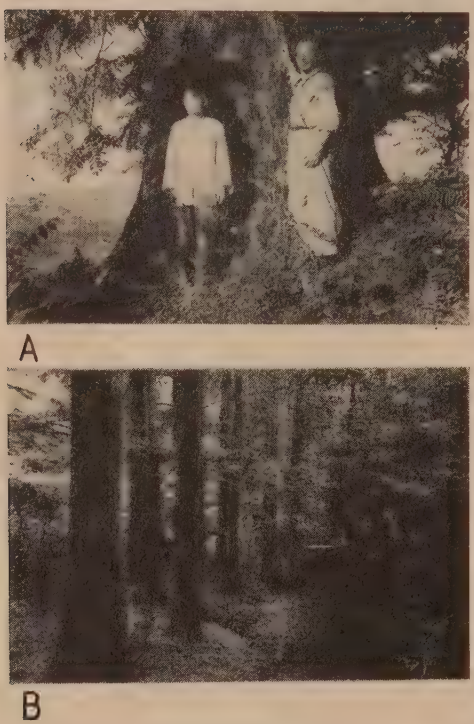

Fig. 5. A. Base of the large tree near Wang-chia-ying. B. A natural grove of Metasequoia in Shui-hsa valley.

In Shui-hsa valley Metasequoia finds its natural habitat in side ravines descending to the valley floor. Following a ravine or side valley down the mountain slope from either side one is sure to find Metasequoia trees at the lower end. They thrive particularly along the banks of small streams, among rocks and boulders covered thickly by liverworts and mosses, occurring usually in small groups or short lines (fig. 5B). With them grows a variety of other trees, and in many places there is a dense thicket-like growth of shrubs and woody lianas. These growths are often very difficult to penetrate; inside them it is much cooler, darker, and wetter than without. In such places Metasequoia reproduces naturally. The habitat as described above is strongly reminiscent of that of blue spruce (*Picea pungens* Engelm.) in the Rocky Mountains of Colorado, U. S. A. Metasequoia grows also in seepage areas at the foot of the slopes where there is abundant shade and moisture. The tree is found upon the valley floor itself, but here it has obviously been planted.

Quadrat Studies

To obtain more accurate knowledge concerning Metasequoia in its home a quadrat study was undertaken. The main purpose was to discover what species of trees, shrubs, and herbs are associated with Metasequoia in its natural habitat, and the relative proportions of these. No

TABLE II. *Density and presence for tree species on ten 10 × 10 m quadrats*

	Density						Presence
	Size-classes					All classes	
	I	II	III	IV	V		
Metasequoia glyptostroboides Hu and Cheng	16	17	4	7	18	62	10
Cunninghamia lanceolata Hook.	18	7	1	7	7	40	8
Castanea Sequinii Dode	5	11	3	6		25	7
Liquidambar formosana Hance	8	7		7		22	6
Rhus (3 spp.)	1	12	1	3		17	6
Cornus controversa Hemsl.	1	5		3	2	11	4
Lindera glauca Bl.	1	7				8	6
Meliosma Oldhami Miq.	1	5		1		7	4
Acer Davidii Fr.	3	3	1			7	4
Styrax japonica S. and Z.		5		1		6	3
Idesia polycarpa Maxim.		3		1		4	2
Populus adenopoda Maxim.	1	1			2	4	3
Nyssa sinensis Oliv.	1	2				3	2
Prunus sp.	1	2				3	2
Kalopanax pictus Nakai		2		1		3	2
Clerodendron mandarinorum Diels		1		2		3	1
Taxus chinensis Rehd.	3					3	1
Pterocarya paliurus Skan.	1				1	2	1
Morus sp.		2				2	2
Quercus variabilis Bl.		2				2	2
Torricellia angulata intermedia Hu		2				2	1
Salix (2 spp.)		2				2	1
Cercidiphyllum japonicum sinicum R. and W.				1		1	1
Betula luminifera Winkl.			1			1	1
Carpinus Fargesii Fr.		1				1	1
Ficus heteromorpha Hemsl.		1				1	1
Litsea elongata Hook.		1				1	1
Total	61	101	11	40	30	243	
Ratio, Metasequoia/total	.20		.36	.18	.60	.26	

attempt was made to identify and distinguish plant communities; a comprehensive survey of the whole region would be essential for this. Another important aim was to gain information as to the reproducing ability of Metasequoia in its natural habitat.

Ten 10 x 10 m quadrats were laid out in areas in which Metasequoia was important (locations indicated on map, fig. 2). Selection of sites was determined by apparent approximation to natural condition, and the area over which the quadrats were distributed coincided roughly with the region in which such conditions were found. The quadrats were placed along the foot of the mountain slopes on both sides of the river. A secondary quadrat (2 × 8 m) was laid inside each major one for the counting of shrubs and seedling trees, and a still smaller one (0.25 × 4 m) for herbs; but the density values of the shrubs and herbs were very variable and apparently of little significance and are therefore not given here.

For the tree species five size-classes were distinguished: I, seedlings less than 1 foot tall; II, seedlings more than 1 foot tall; III, trees 1–3 inches in diameter; IV, trees 4–9 inches in diameter; V, trees 10 inches or more in diameter. Density (number of individuals in the 1000 square meters of the ten quadrats combined) has been computed for each species and each size-class of a given species, and also presence (number of quadrats in total of ten in which a species occurs). The data are presented in table II.

The following trees, not occurring in the quadrats, but mostly close to them, are close associates of Metasequoia:

Cephalotaxus Fortunei Hook.
Fagus longipetiolata Seem.
Quercus acutissima Carr.
Sassafras tsumu Hemsl.
Tapiscia sinensis concolor Cheng
Ulmus multinervis Cheng

The large number of tree species making up the assemblage of which Metasequoia is a constituent—27 species occurring in 1000 square meters and 6 others nearby—is a striking point. Of the 33 species, only four are gymnosperms. As to average spacing of individuals, there is one of diameter 10 inches to each 33 square meters. Those of 1–9 inches diameter are spaced one to each 20 square meters. Seedlings occur one to each 6 square meters. The picture is of a forest of moderate density as to mature trees and rather poor in reproduction. Five species are represented by individuals 10 inches + in diameter—Metasequoia, Cunninghamia, Cornus, Populus, and Pterocarya. Fourteen are represented by individuals 4 inches +—in addition to the above, Castanea, Liquidambar, Rhus, Meliosma, Styrax, Idesia, Kalopanax, Clerodendron, and Cercidiphyllum. Eleven species are represented by seedlings only.

The species of outstanding importance, so far as the quadrats show, are obviously Metasequoia, Cunninghamia, Castanea, and Liquidambar—two gymnosperms and two angiosperms. They comprise 74% of the three upper size-classes and 54% of the seedling classes. Moreover, they are for the most part well represented in all size-classes, indicating that their present preeminence will be maintained. In presence they rank as high or higher than any in the list. The remaining species, definitely less important in the quadrats, are common in the region. It is impossible to foretell the future of those species that are represented entirely or mainly by seedlings. The individuals may be merely "accidentals"; on the other hand, some of them may indicate a successional trend, probably secondary, that will in time result in modification of the composition of the forest.

Turning to Metasequoia in particular, it is plain that this species is the most important one in the assemblage. Of the total comprising size-class V it makes 60%, and most of these individuals are 24–36 inches in diameter. In the combined seedling classes it makes only 20%, but it surpasses every other single species. It is represented in every size-class. All the evidence indicates that it will continue to maintain itself as an important member of the forest assemblage.

Nearly fifty species of shrubs and lianas were found in the ten quadrats. They were very unevenly distributed. In a few quadrats the shrub layer was dense and luxuriant, one providing a list of twenty species. In others the layer was thin and poor in species; severe disturbance is apparently the cause of this condition. The most common erect shrubs were species of Spiraea, Hydrangea, Viburnum, Morus, Berberis, Cudrania, Elaeagnus, Cotoneaster, Rhamnus, and *Lonicera pileata* Oliv. The important woody lianas and liana-like shrubs were Hedera, Rosa, Rubus, Parthenocissus, Akebia, Actinidia, Dalbergia, Lonicera spp., Holboellia, and Schisandra. Hedera, an epiphytic liana, is the commonest of all and is closely associated with Metasequoia. Many of the lianas are armed with spines. The woody lianas, together with a few herbaceous ones, are woven into a tangled mass which affords effective protection to tree seedlings and shrubs. A conspicuous growth of lianas always indicates a dense shrub layer with good reproduction of Metasequoia. Table III is a list of the shrubs and woody lianas found in the ten quadrats. The irregular distribution of the shrubs and lianas is indicated by the figures for presence. The list is a long one (47), but only 6 species occur in half or more of the quadrats, and 19 occur in one only.

Herbaceous plants were found to be even more irregularly distributed than

TABLE III. *Presence values for shrubs and woody lianas, on ten 2 × 8 m quadrats*

	Presence
Hedera nepalensis sinica R. and W.	10
Spiraea japonica Fortunei Rehd.	8
Hydrangea strigosa Rehd.	6
Viburnum ichangense Rehd.	6
Morus alba L.	5
Berberis sp.	5
Rosa Henryi Boul. (spiny vine-like shrub)	4
Rubus setchuenensis Bur. and Fr. (spiny vine-like shrub)	4
Parthenocissus tricuspidata Planch. (liana)	4
Akebia trifoliata Koidz. (liana)	4
Actinidia chinensis Planch. (liana)	4
Cudrania tricuspidata Bur.	4
Elaeagnus sp.	4
Cotoneaster horizontalis Decne.	4
Rhamnus utilis Decne.	3
Evonymus alata Regel.	3
Lonicera pileata Oliv.	3
Camellia oleifera Abel.	3
Pyracanthus Fortuniana Li	2
Meliosma pendens R. and W.	2
Smilax sp. (liana)	2
Coriaria sinica Maxim.	2
Phyllanthus flexuosus Muell.-Arg.	2
Ardisia crispa A. DC	2
Dalbergia stenophylla Prain (spiny liana)	2
Lonicera similis Hemsl. (liana)	2
Evodia officinalis Dode	2
Decaisnea Fargesii Fr.	2
Holboellia sp. (liana)	1
Lonicera japonica Thunb. (liana)	1
Actinidia callosa Henryi R. and W. (liana)	1
Ficus foveolata Wall. (liana)	1
Schisandra pubescens Hemsl. and Wils. (liana)	1
Helwingia japonica Dietr.	1
Corylopsis sinensis Hemsl.	1
Mallotus tenuifolia Muell.-Arg.	1
Picrasma quassioides Benn.	1
Nothopanax Davidii Harm.	1
Dichroa febrifuga Lour.	1
Hibiscus syriacus L.	1
Viburnum setigerum Hance	1
Euphorbia sp.	1
Lespedeza sp.	1
Callicarpa sp.	1
Buddleja sp.	1
Berchemia sp. (liana)	1
Bamboo	1

were the shrubs. They were particularly sparse where the shrub layer was dense, the only herbs found in such places being climbing species of Rubia and certain legumes. A few of the quadrats had several species of large ferns and tall herbs including Impatiens, Polygonum, Urtica, Pilea, Boehmeria, Carpesium, Geum, Phryma, and Iris. Others were crowded with smaller herbs: Houttuynia, Codonopsis, Commelina, Carex, Kyllinga, Geranium, Saxifraga, Chloranthus, Fagopyrum, Oxalis, and many others. One quadrat, placed on muddy seepage ground, was covered by a soft carpet of *Diarrhena* sp., a delicate grass. Liverworts and mosses were abundant in certain places. Nearly one hundred species of herbs, including the lower forms, have been collected from the areas in which Metasequoia grows. There is apparently nothing distinctive in this flora, and the brief description given above seems adequate for the present purpose.

NOTES ON ECOLOGICAL LIFE HISTORY

In an environment such as has been described the seeds of Metasequoia germinate. Seedlings are found in crevices between rocks and boulders and in moist sandy places. In the thicket-like growth beneath the forest trees are seedlings and young saplings up to 3 m tall. As they grow larger they encounter serious interference from the lianas that are so thickly interlaced among the trees and shrubs. Other tree species are usually rigid enough to penetrate the mass without much difficulty. The stems and branches of Metasequoia, however, are flexible, and are bent over and deformed by the load of liana stems. The struggle to get through is a keen one. Such conditions are certainly not ideal for successful reproduction. Metasequoia, however, is evidently very shade-tolerant, and the dense thicket growth gives it a certain amount of protection from biotic dangers. It appears that such an environment, in spite of its disadvantages, provides perhaps the only conditions under which it can, at the present time, successfully reproduce.

Having finally penetrated the shrub-liana layer, Metasequoia, which probably has a faster growth rate than its companion species, develops rapidly, finally standing out conspicuously above them and recognizable at a great distance by its bright green color.

The mature tree (figs. 4, 5, 6) has been well described by Hu and Cheng ('48: 155–156). Since this publication is not readily accessible in the United States, their characterization is quoted here so far as it applies to the major vegetative features:

"Tree to 35 m tall with a tapering trunk strongly buttressed at the base, to 2.3 m in diam. B. H., pyramidal when young, in old age usually spreading with broadly rounded crown; bark dark gray, fissured, peeling off in long threads in old age, exfoliating in thin plates exposing the purplish brown inner bark beneath while young, branchlets opposite, glabrous, smooth, green when young becoming

FIG. 6. *Metasequoia glyptostroboides:* branch, cones, bark.

brownish later and changing to brownish-gray or gray in the second or third year; lateral foliage shoot deciduous in winter, glabrous, opposite, to 7 cm long, distichously arranged, with persistent bracts at the base, without both terminal and axillary buds; winter buds ovoid or ellipsoid, obtuse, 4 mm long, 3 mm across, glabrous; . . . leaves deciduous, opposite, distichously arranged in two ranks, linear, 8–15 mm long, 1.2 mm broad at the middle, broader toward the base, sessile or nearly sessile, midrib elevated on both sides, bluish-green above, light green and with 4–6 rows of stomata on each side below."

According to Chaney (personal communication) increment cores suggest for the largest trees an age of at least 300 years.

The senior author made the following additional observations in 1948. Generally the Metasequoia trees in Shui-hsa valley are 6–9 dm in diameter; medium-sized trees are uncommon. The largest tree measured, an isolated individual near Wang-chia-ying (figs. 4C, D; 5A), was 2.22 m in diameter, the diameter of its buttressed base close to the ground 3.31 m, height of trunk to first branch 8 m, total height about 50 m, spread of branches 13.1 m. Trees growing in comparatively open situations are branched almost to the ground. In Shui-hsa valley the bark is heavily coated with moss, and epiphytic ferns grow on the main horizontal branches.

Influence of Man

The present local distribution of Metasequoia has been much influenced by man, through destruction and also by planting. Its occurrence as an important forest constituent was once far more widespread than now, as is indicated by isolated big trees at considerable distances from Shui-hsa-pa. The type tree at Mo-tao-chi is 35 km distant and the big tree near Wang-chia-ying more than twenty. Such trees, three centuries old at least, must antedate the initiation of agricultural activity in the valley. After the natural vegetation had been displaced or profoundly modified because of agricultural use, effective reproduction was no longer possible. The natives apparently venerated the biggest trees and therefore protected them. It seems quite natural that the first permanent settlers in the region should recognize in the tree something different, unusual, and worthy of special respect. A small temple stands beside the type tree at Mo-tao-chi. In neighboring valleys the natural communities of which Metasequoia was a constituent have been completely destroyed in the last two centuries. In Shui-hsa valley destruction has been only partial—but it still goes on. It seems certain that even before the period of destruction the stands of Metasequoia were discontinuous, occupying mainly ravines and stream banks as they do today.

In Shui-hsa valley there has been considerable planting of Metasequoia. Natives are constantly removing good-sized seedlings and saplings from their native sites. Small trees are growing along the banks of the main stream in straight rows. They are also seen on the margins of the rice paddies, along roadsides, and in home yards.

In view of the common practice of transplantation it is not surprising that stands of uncertain origin occur which may be hardly distinguishable from natural stands. Some of these consist of groups of 10 to 30 mature trees that appear as if they had had a natural origin. The site, however, is not the normal one. It is drier, the floor is clearer, and conditions are not favorable for reproduction. On the other hand, there are many natural stands so altered by man that they appear as planted.

It is not clear why the natives plant so extensively a tree that is of little economic importance to them. There is no systematic tree culture in Shui-hsa valley. A few trees of economic value are planted: *Magnolia officinalis* R. and W., the bark of which is used as a medicine, *Juglans cathayana* Dode for the nuts, *Rhus verniciflua* Stokes for lacquer. *Cunninghamia lanceolata* Hook. is regarded as the best timber tree of the region, but it is not planted. Metasequoia is sometimes used

for fuel and in construction, but its wood is not considered to be of good quality. Aside from these rather incidental uses, the reason for planting Metasequoia must be mainly an aesthetic one.

The fate of Metasequoia rests with man. If destruction continues, all the native stands will be eliminated. The massive veterans will ultimately die, leaving only the planted trees surviving—the same fate that has already overtaken Ginkgo.

Conclusion

It is assumed that climatic change and other causes have brought about the restriction of Metasequoia to the general area—about 800 sq km—where natural-grown individuals are found today. Within this small area there is further limitation of occurrence on the basis of soil character, soil moisture conditions, and microclimate. The tree is partial to slightly acid or circumneutral soils derived from sandstone; it avoids soils of limestone origin in areas that appear to be otherwise suitable. Moist soil and humid atmosphere seem to be essential for successful reproduction. These various conditions are fulfilled in narrow ravines and seepage grounds; the tree is essentially a member of a stream-bank community. The evidence for these conclusions comes from Shui-hsa valley, a very small part of the whole range of the species.

The scattered individuals of considerable or large size growing beyond the confines of the valley need to be accounted for. It seems necessary to conclude that conditions like those in Shui-hsa valley existed elsewhere nearby in the none too distant past; that in favorable spots reproduction of Metasequoia was possible recently enough to have given rise to the existing mature trees. Increase of human population, with consequent exploitation of the natural resources of the area, has resulted in general destruction of the conditions essential for reproduction of Metasequoia; a certain number of mature individuals survive.

Only in Shui-hsa valley does Metasequoia exist under an approximation to natural conditions. This may be due in part to certain environmental advantages. The valley lies at a somewhat higher elevation than others in the sandstone region, it is narrower, and certain features of its local climate seem to be in its favor. More important, probably, is the fact that this valley was the last to be occupied by permanent settlers, the period of occupation extending back only two centuries. Late settlement is doubtless due to its higher altitude, the comparatively small area favorable for rice culture, possibly poorer soil, and particularly its unique character as a basin completely enclosed by mountains, with no easy river route into it. Increase of population pressure outside finally became the incentive leading to its occupation. Shorter period of occupation and sparser population have permitted Metasequoia to remain here in an approximately natural state.

It is gratifying to know that a "Metasequoia Conservation Committee" has been formed in China. Its honorary chairman is Dr. Hu Shih, former ambassador to the United States; its chairman is Mr. Wong Wen Hao, former Premier of China and a noted geologist. It is to be hoped that the efforts of these Chinese scientists to preserve the natural stands of Metasequoia through the establishment of a national park or some other form of nature reservation will, in spite of formidable difficulties, be crowned with success before it is too late.

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NOTES AND COMMENT

ECOLOGY AND DISTRIBUTION OF THE SHREW *SOREX DISPAR* IN PENNSYLVANIA

The only records of *Sorex dispar* Batchelder in Pennsylvania prior to 1946 were from Sullivan, Luzerne and Berks counties in the eastern part of the state (Hamilton, '43). Since July, 1946, the Pennsylvania Game Commission, with the cooperation of the Section of Mammals of Carnegie Museum, Pittsburgh, has been conducting a survey of the mammals of the state under the Federal Aid in Wildlife Restoration program. The authors, as leaders of Pittman-Robertson projects 20-R and 24-R in the western part of the state, collected this shrew in seven localities. In addition to our own observations, we have used the field notes of our assistants, John J. Christian, Woodrow W. Goodpaster, and Harvey A. Roberts. The records of this shrew in central Pennsylvania have been supplied by Clay L. Gifford and Harry R. Roslund, the leaders of Pittman-Robertson projects 37-R and 38-R. This paper summarizes all of our observations from July 1946 to July 1949 on the distribution and ecology of this shrew in Pennsylvania.

Distribution

The locality records shown in table I extend the known range of *Sorex dispar* westward in Pennsylvania into the Allegheny Plateau and the Allegheny Mountains and show that the range is continuous across the state. These records indicate that the range of *dispar* is probably continuous in the mountains from New Hampshire to southern West Virginia. Its occurrence in the talus slopes in the Ridge and Valley Province suggest that it may occur in these ridges in western Virginia. Figure 1 shows the distribution of *Sorex dispar* in Pennsylvania.

Table I. *Localities in Pennsylvania where* Sorex dispar *were collected 1946–1949*

County	Town	Altitude	Males	Females
Clearfield	McGees Mills	1300′	1	
Huntingdon	2 mi. NE Spruce Creek	900	1	1
Jefferson	5½ mi. NE Sigel	1640	5	4
Somerset	½ mi. NW Bakersville	2300	1	
Union	1 mi. S. Glen Iron	1400	1	
Venango	6 mi. E Oil City	1120		1
Venango	4 mi. S Franklin	1240	1	
Westmoreland	2 mi. SE Rector	1600	1	3
Westmoreland	4 mi. SE Latrobe	1060	4	
Westmoreland	½ mi. Se Laughlintown	1400	2	

Habitat

Jackson ('28) says of the habitat of this shrew, "Habitat records of the rare *Sorex dispar* would indicate that the species usually lives among rocks." He cites Batchelder ('96): ". . . the type specimen was trapped among some large, angular rocks at the head of a wooded talus of loose rocks just below low cliffs which shaded the spot and kept it cool."

Our studies indicate that this description of the type locality is also an accurate description of the limited ecological niche occupied by this species throughout its range. *Sorex dispar* is apparently restricted to cool, moist talus in woods. In the localities where this shrew was collected, it was restricted to areas where there was a mantle of loose rock two to thirty feet deep. The surface of the talus was partially or completely covered with a mat of leaf mold and tangled roots. In such places the moving of a rock or log would expose a labyrinth of passages extending in all directions among the rocks. With two exceptions all of the animals were trapped in such talus accumulations; the exceptions were taken on sandy clay soil in the vicinity of talus. Most of the animals were taken in traps placed approximately one foot below the surface in the spaces between the rocks.

In the folded strata of central Pennsylvania, the talus slopes of quartzite are vast in extent, covering entire mountains and extending along them for miles. But in western Pennsylvania where the strata lie horizontally, accumulations of talus are limited to ravines and relatively small local accumulations below outcrops of the more resistant sandstones and conglomerates.

There is no evidence that *S. dispar* is restricted by altitude in Pennsylvania, for it has been found at elevations from 900 ft. to 2,300 ft. In Westmoreland County all the stations where *S. dispar* was taken were in valleys at elevations between 1,000 ft. and 1,600 ft. along the western base of Laurel Mountain. The highest locality, 2,300 ft., was about half way up the eastern slope of Laurel Mountain in Somerset County. Several habitats on top of Laurel Mountain that appeared equally suitable were trapped with negative results. In Venango County, *S. dispar* was found in two localities, one at stream level (1,120 ft.) and the other near the top of a hill at 1,240 ft., and the locality where they were collected in Jefferson County was on top of a knob at 1,640 ft.

All localities where these animals were taken were wooded, but the type of forest varied from the cool dark forests of mature hemlock and yellow birch to the relatively warm, dry forests of red oak, chestnut oak and rep maple. However, the portion of the habitat occupied by *S.*

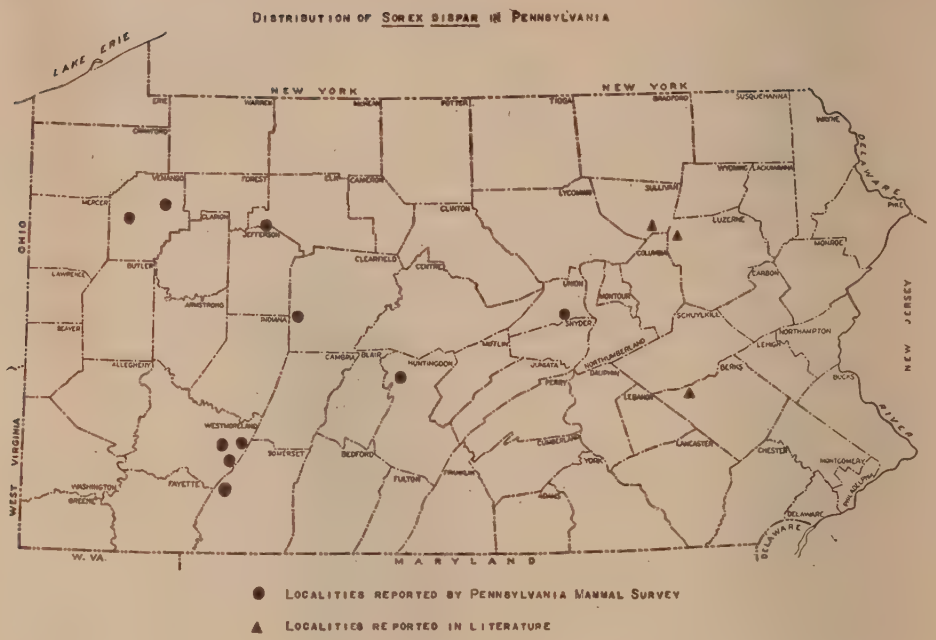

FIG. 1.

dispar is not subject to these variations since the extensive habitat down in the rocks is cold and dark and constitutes a remarkably uniform environment. This type of habitat is unique in having the lowest summer temperature of any habitat in the eastern United States. In parts of such formations the temperature may remain below freezing all summer as it does in the "Ice Caves" of Huntingdon County, the "Ice Mine" in Potter County, Pennsylvania, and in the "Ice Mountain" in Hampshire County, West Virginia.

In one locality (5½ mi. NE of Sigel) where 9 of these shrews were collected, 6 were taken in traps 7 to 14 inches below the surface; 3 were taken on small ledges on the face of the rock outcrop at heights of 2 to 6 feet above the surface of the ground. Although many traps were placed 15 to 27 inches below the surface, no *S. dispar* was taken.

Associated Mammals

Red-backed mice (*Clethrionomys*) were taken in every locality where *S. dispar* was collected, and although not restricted to rock slides, they were generally more numerous there than in the other habitats in the same locality.

In six localities *S. dispar* was associated with three other shrews: *Sorex cinereus cinereus* Kerr, *Sorex fumeus fumeus* Miller and *Blarina brevicauda brevicauda* (Say). Of these, *S. c. cinereus* was the most numerous and appeared to have habits most similar to those of *S. dispar*.

Food

The digestive tracts of three *S. dispar* collected in April from one locality were examined. All of the stomachs contained centipedes. The intestines also contained mostly centipede remains although there were traces of both insects and spiders. For comparison, eight stomachs and intestines of *S. cinereus* from the same locality and month were examined. Spiders were the principal food of these specimens, with beetle remains next in importance and traces of other insects and insect pupae. No centipedes were found in either stomachs or intestines of *S. cinereus*. This difference may not be significant, but it suggests that *S. dispar* may have more specialized food habits than *S. cinereus*.

Reproduction

Of the nine females trapped, only four showed any indication of reproductive activity. Two specimens trapped in northern Jefferson County, April 26 and 28, 1948, had enlarged uteri although there was no evidence of embryos or placental sites. These were not examined microscopically, but in each the appearance of the uterus was that associated with oestrus. Two other specimens from the same locality, trapped May 3 and 6, 1948, were both pregnant, each with 5 embryos. In each, the embryos were still too minute to measure (less than 0.5 mm.), and the longest dimension of the fetal membranes plus the thickened uterine wall was 2 mm.

TABLE II. *Reproductive data for three species of* Sorex *from 5½ mi. NE Sigel*

	Embryos	Size and remarks
Sorex dispar		
April 26, 1948	0	uterus enlarged . . . oestrus?
April 28, 1948	0	uterus enlarged . . . oestrus?
May 3, 1948	5	less than 0.5 mm. long
May 6, 1948	5	less than 0.5 mm. long
Sorex fumeus fumeus		
April 17, 1948	5	less than 1 mm. long
April 29, 1948	6	approximately 3 mm. long
May 5, 1948	2	approximately 3 mm. long
Sorex cinereus cinereus		
April 23, 1948	7	8 mm. long
April 23, 1948	7	not measured
April 29, 1948	8	less than 1 mm.
May 3, 1948	8	10 mm. long
May 5, 1948	6	9 mm. long
May 31, 1948	5	4 mm. long

The other five females were taken in February, March and July and showed no evidence of reproductive activity.

Table II compares the reproductive data for *S. dispar* with those for *S. fumeus* and *S. cinereus* taken in the same locality during April and May, 1948. The length given is the crown-rump measurement of the foetus in normal flexed position.

MEASUREMENTS

Males tend to be somewhat heavier than the females. The maximum weight for females was 5.5 grams, but of the 17 males, only 3 weighed less than 5.5, and 4 weighed over 6 grams. In other measurements the two sexes were identical.

The average measurements of 17 males, and the range of measurements, were, in millimeters: total length 120 (111–128); tail 57 (54–60); hind foot 14.6 (13–15); ear 9 (8–10); weight 5.5 grams (3.9–8.3).

The corresponding measurements of 9 females: total length 120 (110–128); tail 57 (54–60); hind foot 14.5 (14–15); ear 9.2 (9–10); weight 4.7 grams (3.5–5.5).

The vibrissae of *S. dispar* are conspicuously longer than those of *S. cinereus* and *S. fumeus*. The longest vibrissae of *S. dispar* are 22–23 millimeters long, while those of *S. cinereus* and *S. fumeus* are usually less than 21 millimeters long.

The ear of *S. dispar* averages slightly larger than either *S. fumeus* or *S. cinereus*. The following averages are those for 8 *S. dispar* and 10 each of the other two shrews all collected in the same locality and measured to the nearest millimeter by the same person: *S. dispar* 9.4 (9–10); *S. fumeus* 8.4 (8–9); *S. cinereus* 7.7 (7–9).

DISCUSSION

The three species of *Sorex* occurring together may be arranged in the order of their degree of dependence upon a specialized habitat. *Sorex cinereus* is the most adaptable and overlaps the habitats of both *S. dispar* and *S. fumeus*. *Sorex fumeus* appears to prefer areas of either deep leaf mold or true soil and does not inhabit the talus slopes to the same extent as does *S. cinereus*. *Sorex dispar* appears to be restricted to the deep accumulations of rocks and is rarely taken away from this type of habitat.

Associated with the specialized habitat requirements of *S. dispar* are structural modifications that make this shrew especially adapted to foraging among rocks. Although intermediate in size between *S. cinereus* and *S. fumeus*, *S. dispar* has longer hind feet, a much longer tail, slightly larger ears, and longer vibrissae than either of the other shrews. Howell ('26) found similar modifications in the wood rat, subgenus of *Neotoma*, that lives in rock slides, and he states, "It may be presumed that the longer vibrissae of *Teonoma* have been developed to serve as a better tactile organ in the dark intricacies of the rock slides which are frequented by that animal."

Our trapping records indicate that *S. dispar* is not common. However, this may reflect variations in behavior that bring these shrews in contact with traps more at some times than at others. The nature of their habitat is such that it has considerable depth as well as area so that the usual methods of intensive trapping are of little value since it is impossible to saturate the habitat with traps.

Some idea of the possible density of these shrews is shown by the traplines 5½ miles NE of Sigel. Out of a total of nine *S. dispar*, seven of them were in an area of approximately one acre. Four were taken in 24 hours, two at night, and two in the afternoon, and two were taken by the same trap. Five were taken in the first 48 hours in twenty traps, and the remaining four were taken in the following 10 days of trapping with up to two hundred traps. All nine were taken in an area 0.4 of a mile long, and approximately 100 feet wide, along the base of a sandstone ledge.

That five of the nine shrews were taken in the first 48 hours in less than a fifth of the total area subsequently trapped indicates either an unusual concentration of these shrews or a period of heightened activity that increased the frequency of their contacts with traps. Either could be the result of a change in feeding behavior or increased activity associated with breeding. It is probably significant, however, that of the first four, two were females that were apparently in oestrus, and the two females trapped in the same locality 10 days later were both in early stages of pregnancy.

Further evidence that changes in the habits of the shrew are important in effecting their capture is the seasonal distribution of the catch. When the number of *S. dispar* collected in each

TABLE III. *Number of* Sorex dispar *collected in each locality arranged by months*

Month	Collections	Totals
January	0	
February	2, 1, 1	4 specimens in 3 localities
March	1	1 specimen in 1 locality
April	6, 3, 2, 1, 1	13 specimens in 5 localities
May	3, 1, 1	5 specimens in 3 localities
June	0	
July	2	2 specimens in 1 locality
August	0	
September	0	
October	1	1 specimen in 1 locality
November	0	
December	0	

locality is arranged by months, it is apparent that April leads in the number of collections as well as in the number of shrews in each collection. This is shown in table III. Of the 26 collected, 23 were trapped in the 4 months of February to May. Since most mammal collecting is usually done in the summer months, this may account for the reputed rarity of *Sorex dispar*.

All of the specimens collected have been deposited in the Pennsylvania Mammal Survey Collection in the Section of Mammals, Carnegie Museum, Pittsburgh, Pennsylvania.

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A CONTRIBUTION TOWARDS THE STUDY OF THE DISPERSAL MECHANISMS IN FLOWERING PLANTS OF MYSORE (SOUTH INDIA)

In a recent paper, the author (Razi, '46) gave a check list of the flowering plants of Mysore embodying the field survey carried out for several years. An attempt was made to indicate the life forms of 2,379 species of flowering plants reported therein on the basis of Raunkiaer's system. Studies on the dispersal mechanisms of the flowering plants of Mysore were also taken up with a view to get a better understanding of the plant distribution. In the present paper an account of the result of the studies on the dispersal mechanisms involved in plant distribution in Mysore is presented.

In studying the dispersal mechanisms, the method of analysis suggested by Agharkar ('20) is adopted. Two main groups of dispersal mechanisms are recognized; the "Active" and the "Passive," depending on whether the plant is directly concerned in modifying its fruit structure to suit the mode of dispersal, or whether an extraneous agency partakes in this process. Plants having the active mode include those with explosive fruits and others showing a mechanical contrivance for dispersal. In contrast, the second category includes plants with dispersal mechanisms through the agency of wind, water, animals, etc.

The following outline indicates the main headings under which the dispersal mechanisms are treated.

A. Active mode of dispersal: Fruits with arrangements for scattering the seeds.
- *1 a.* The explosive mechanism rests in the peculiar structure of the pericarp.
- *1 b.* The explosive mechanism rests in building peculiar organs (jaculators, etc.) for scattering the seeds.

B. Passive mode of dispersal: Disseminules (fruits or seeds) with special contrivances.
- *a*) Dissemination through wind, due to:
  - *2.* Small size of the fruit or seed.
  - *3.* Formation of wings on fruit or seed.
  - *4.* Presence of hairs on fruit or seed.
  - *5.* Other apparatus like bladder fruit, tumble weed, etc.
- *b*) Dissemination through water. This includes:
  - *6.* Rainwash, river or sea drift.
- *c*) Dissemination through animals.
  - *7.* Endozooic; where the animals concerned swallow and pass them.
  - *8.* Epizooic; where the fruits or seeds stick to the body of the animals and are thus transported.

d) Plant introduction by man, intentional or unintentional.

In the following analysis only the generic names will be mentioned in order to conserve space, and the number of species included under each genus is already given in the check list published previously (Razi, '46). The numbers following certain names indicate the alternate dispersal mechanism in the genus. The heading *d*) has not been dealt with here, since this would include all agricultural and horticultural plants, which have been omitted from consideration. However, where it is known that man was responsible for the introduction of the species concerned (as, e.g., in *Lantana, Physalis, Croton sparsiflorus*) this has been indicated in parentheses.

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Analysis of Dispersal Mechanisms

A. Active mode of dispersal.

1 a. The explosive mechanism rests in the peculiar structure of the pericarp.

Cardamine (*8*), Viola (*8*), Helicteres, Oxalis (*6*), Biophytum (*6*), Impatiens (*6*), *Rhynchosia* (*2*), *Flemingia, Parkinsonia, Bauhinia,* Agrostistachys, Ricinus.

The genera printed in italics have pods which open by torsion.

1 b. The explosive mechanism rests in building peculiar organs (jaculators, etc.) for scattering the seeds.

Andrographis, Haplanthus, Gymnostachyum, Lepidagathis, Rungia, Dicliptera, Ecbolium, Justicia, Adhatoda, Rhinacanthus, Peristrophe, Thunbergia, Nelsonia, Meyenia, Staurogyne, Cardanthera, Ruellia, Hygrophila, Micranthus, Dyschoriste, Eranthemum.

B. Passive mode of dispersal.

a) Dissemination through wind, due to:

2. Small size of the fruit or seed.

Hypericum, Rothia (*3*), Heylandia (*3*), Psoralea (*3*), Eleiotis (*3*), Pycnospora (*3*), Teramnus (*3*), Spatholobus (*3*), Cyclista (*2*), Rhynchosia (*1*), Calpurnea, Pterolobium (*3*), Acrocarpus (*3*), Hardwickia (*3*), Kingiodendron (*3*), Vahlia, Parnassia, Klugia (*6*), Rhyncoglossum (*6*), Homalium Neonauclea (*3*), Adina (*5, 6*), Wendlandia (*3*), Hymenodictyon (*3*), Dentella, Knoxia (*3*), Exacum (*6*), Enicostemma (*6*), Erythraea (*6*), Gentiana (*6*), Hoppea (*6*), Canscora (*6*), Limnanthemum (*6*), Swertia (*6*), Evolvulus (*6*), Verbascum, Celsia, Sutera, Mazus, Adenosma, Stemodia, Dopatrium, Torenia, Vandellia, Sopubia, Centranthera, Rhamphicarpa, Micrargeria, Calceolaria, Celosia, Banalia, Allmania, Digera, Plecospermum, Streblus, Girardinia (*6*), Elatostemma (*6*), Procris (*6*), Pilea (*6*) Pellionia (*6*), Pouzolzia (*6, 7*), Burmannia, Oberonia, Microstylis, Liparis, Desmotrichum, Dendrobium, Didymoplexis, Bulbophyllum, Cirrhopetalum, Chrysoglossum, Porpax, Josephia, Coelogyne, Pholidota, Calanthe, Arundina, Eulophia, Cymbidium, Geodorum, Polystachya, Luisia, Rhynchostylis, Chilochista, Aerides, Vanda, Saccolabium, Diplocentrum, Torpidia, Anoectochilus, Zeuxine, Aphyllorchis, Nervilea, Epipogum, Habenaria, Peristylus, Platantherа, Disperis, Satyrium, Kyllinga (*7*), Eleocharis (*7*), Bulbostylis (*7*), Fuirena (*7*), Lipocarpha (*7*).

B. a) *3.* Formation of wings on fruit or seed.

Winged fruit is seen in: Dipterocarpus (*6*), Vatica (*6*), Shorea, Hopea, Pterospermum (*5*), Eriolaena, Melhania, Hiptage, Ailanthus, Hippocratea (*6*), Ventilago, Gouania, Hydrocotyle (*6*), Centella (*6*), Polyzygus (*6*), Heracleum (*6, 8*), Ellertonia, Holarrhena, Paracaryum (*8*), Gyrocarpus (*6*), Holoptelea, Casuarina (man), Eriocaulon (*6, 8*), Dioscorea.

Winged seed is met with in: Gordonia, Aspidopterys, Rothia (*2*), Heylandia (*2*), Psoralea (*2*), Eleiotis (*2*), Pycnospora (*2*), Teramnus (*2, 8*), Butea, Spatholobus (*2*), Pterocarpus, Derris, Pterolobium (*2*), Acrocarpus (*2*), Hardwickia (*2*), Kingiodendron (*2*), Terminalia (*7*), Anogeissus, Combretum, Lagerstroemia, Lawsonia, Zanonia, Neonauclea (*2*), Wendlandia (*2*), Knoxia (*2*), Vallaris, Wrightia, Aganosma, Anodendron, Ichnocarpus, Tabernaemontana, Linaria (man), Aeschynanthus, Oroxylum, Millingtonia, Dolichondrone (*6*), Heterophragma, Stereospermum, Radermachera, Pajanelia, Spathodea, Symphorema, Sphenodesme, Aristolochia (by sea on a log), Apama.

B. a) *4.* Presence of hair on fruit or seed.

Hair on fruit is seen in: Clematis, Naravelia, Centratherum, Lamprachaenium, Adenoon, Vernonia, Elephantopus, Ageratum (*8*), Centipeda, Dichrocephala, Grangea, Conyza, Blumea, Laggera, Pluchea, Gnaphalium, Blepharispermum, Anaphalis, Pulicaria, Lagasca, Moonia, Flaveria, Gynura, Galnisoga (*6*), Artemisia, Emilia, Notonia, Senecio (*8*), Tricholepis, Dicoma (man, also found in imported wool), Crepis, Sonchus (*6, 8*), Erechthites, Calendulacea, Eupatorium.

Hair on seed occurs in: Cochlospermum, Bombax, Tamarix, Helichrysum (*8*), Alstonia, Parsonsia (*6*), Beaumontia (*6*), Hemidesmus, Cryptolepis, Holostemma, Secamone, Toxocarpus, Genianthus, Cynanchum, Pergularia, Ty-

lophora, Marsdenia, Sarcostemma, Gymnema, Oianthus, Hoya, Brachystelma, Caralluma, Ceropegia, Buddleia, Lasiosiphon (*7*).

B. a) *5.* Other apparatus like bladder fruit, tumble weeds, etc.

Papaver (wind shaken), Pocciloneuron (*3*), Chloroxylon, Naregamia, Munronia, Soymida, Chukrassia, Cedrela (*6*), Cardiospermum (bladder fruit), Smithia, Tetrameles, Begonia (*8*), Adina (*2, 6*), Schrebera, Ligustrum, Campanula, Leucas (*6*, wind shaken), Plantago (*7*, man, membraneous fruit), Imperata, Cleistachne, Saccharum, Dimeria, Pogonatherum, Eulalia, Ischaemum (*6*), Sehima, Lophopogon (*6*), Apocopsis (*8*), Arthraxon, Sorghum (man), Dichanthium (*8*), Iseilema (*8*), Pseudanthistiria (*8*), Cymbopogon, Mnesithea, Hemarthria, Alloteropsis, Oplismenus (*8*), Pennisetum, Isachne, Phragmites, Aristida, Garnotia (*7*), Perotis (*8*), Leptochloa (*6, 7*), Oropetium, Microchloa, Melanocenchris, Tripogon (*8*), Enteropogon (*8*), Cynodon (*6, 7*), Chloris, Teinostachyum, Oxytenanthera, Ochlandra, Pappophorum, Panicum (*8*), Cyrtococcum (*8*), Eragrostis (*6, 7*).

B. b) *6.* Dissemination through water; mostly by rainwash.

Dillenia, Anona (sea), Portulaca (*7*, buoyant seedlings), Ochrocarpus (sea), Mesua, Dipterocarpus (*3*), Vatica, Vateria Cedrela (*5*), Hippocratea (*5*), Dodonea (*5*, man), Sesbania (man), Aeschynomene (*8*), Mucuna (man), Vigna, Dalbergia, Sophora, Cassia (*7*), Entada (*7*), Albizzia, Drosera, Carallia (sea), Terminalia Catappa (sea), Terminalia, Sonerila, Nesaea (*8*), Lagerstroemia (*3*, sea), Jussieua (*8*, man, fragmentation), Bryonopsis (*7*), Trianthema, Orygeia, Mollugo, Gisekia, Hydrocotyle (*3*), Centella (*3*), Polyzygus (*3*), Adina (*3, 5*), Argostemma, Oldenlandia, Anotis, Ophiorrhiza, Borreria, Mundulea (*7*), Exacum (*2*), Enicostemma (*2*), Erythraea (*2*), Gentiana (*2*), Hoppea (*2*), Canscora (*2*), Swertia (*2*), Quamoclit, Stictocardia, Evolvulus (*2*), Convolvulus (*2*), Physalis (*7*, sea), Didymocarpus, Klugia (*2*), Rhyncoglossum (*2*), Pedicularis (*7*), Striga (*7*), Aeginetia (*2*), Christisonia (*2*), Orobanche (*2*), Leucas (*5*), Chenopodium (*7*), Basella (*7*), Myristica (*7*), Gyrocarpus (*3*, sea), Balanophora, Trewia (*7*), Excoecaria, Morus (*7*), Girardinia (*2*), Elatostemma (*2*), Procris (*2*), Pilea (*2*), Pellionia (*2*), Pouzolzia (*2*), Pandanus (*7*, sea), Eriocaulon (*3, 8*), Manisuris (*8*), Saccharum (*5*), Eragrostis (*5, 7*), Cynodon (*5, 7*), Poa, Holcus, Hordeum, Avena, Eleusine (man), Digitaria.

The following genera are dispersed by stream or river currents: Nymphaea, Nelumbium, Nasturtium, Crataeva, Tamarix, Calophyllum (*7*, sea), Hibiscus (*8*, ants, sea), Biophytum (*1*), Ximenia (*5*), Cardiospermum, (*5*, man, bladder fruit), Pongamia, Caesalpinia (sea), Myriophyllum (fragmentation), Barringtonia, Rotala (*8*), Ammannia (*8*), Ludwigia, Trapa (sea), Maba, Limnanthemum, Ipomaea (*7*), Limnophila (*8*), Utricularia (*2, 8*), Dolichondrone, Tectona, Tristicha, Dicraea, Hydrobryum (= Zeylanidium), Acalypha, Homonoia, Hydrilla (*8*), Musa (*7*), Crinum, Tacca, Lagarosiphon (*8*), Vallisneria (*8*), Blyxa (*8*), Ottelia (*8*), Dioscorea (bulbils washed by water), Moschosma, Eichhornia (vegetative multiplication), Juncus (*8*), Areca (man, sea), Cocos (man, sea), Arenga, Corypha Pistia (*8*), Cryptocoryne, Lagenandra, Acorus (vegetative multiplication), Carex (*7*, sea), Scirpus (*7*), Hypolytrum (*7*), Coix (*7*, sea), Chionachne, Digitaria, Echinochloa, Setaria (*8*), Pseudoraphis (*8*), Leersia (*8*) Hygrorrhiza, Dendrocalamus, Lepturus.

B. c). Dissemination through animals.

7. Endozooic dispersal.

These genera are dispersed endozooically by birds: Ranunculus (*6*), Thalictrum (*6*), Michelia (rodents, man), Anona (mammals), Cocculus, Cissampelos (man), Fumaria, Maerua, Capparis, Cadaba, Pittosporum (*6*), Calophyllum (bats), Eurya, Maba, Malvastrum, Sida (ants), Sterculia, Fuirena, Guazuma, Leptonychia, Grewia (bats), Exocarpus (bats, monkeys), Toddalia, Acronychia, Glychosmis, Murraya, Clausena, Luvunga, Paramignya, Atalantia, Ochna, Ouratea, Canarium, Melia (bats), Aglaia, Dysoxylum, Amoora, Lansium, Heynea, Beddomea, Sandoricum, Euonymus (*8*), Pleurostylis (*8*), Elaeodendron (*8*), Scutia, Zizyphus, Vitex, Ampelocissus, Allophylus, Harpullia, Rhus, Anacardium (bats), Rourea, Connarus, Uraria, Ougeinia, Desmodium (*8*, adhesive), Abrus, Shuteria, Dumasia, Glycine, Erythrina, Dalbergia, Ormosia, Pithecolobium, Alysicarpus, Phaseolus (cattle), Pygeum, Rubus, Rosa, Weihea, Blepharistemma, Psidium (bats), Jambosa (bats), Syzygium (bats), Eugenia (bats), Osbeckia, Melastoma, Medinella, Memecylon, Casearia, Passiflora, Trichosanthes (monkeys), Schefflera, Viburnum, Morinda (*6*), Mitragyna, Neurocalyx, Coffea (bats), Stylocoryne, Psychotria, Lasianthus, Chasalia, Saprosma, Hamiltonia, Morinda (*6*), Rubia, Galium, Canthium, Lobelia (*5*), Vaccinium (mammals), Anagallis (adhesion to mud), Ardisia, Chrysophyllum, Mimusops (civets), Diospyros (cattle), Linociera, Olax, Jasminum, Azima, Carissa, Ervatamia, Fagraea, Strychnos (mammals), Ilysanthes, Lindernia, Scoparia (cattle), Cordia, Ehretia, Coldenia, Argyreia, Lettsomia, Erycibe, Cuscuta (*6*), Solanum (mammals), Lantana, Lippia, Stachytarpheta, Bouchea, Callicarpa, Clerodendron, Chenopodium (*6*), Basella (*6*), Polygonum, Gymnacranthera, Knema,

Myristica (*6*), Cryptocarya, Beilschmiedia, Cinnamomum, Alseodaphne, Litsea, Neolitsea, Cassytha, Santalum, Osyris, Scleropyron, Euphorbia (man, *1*), Briedelia (*8*), Cleistanthus (*8*), Actephila (*8*), Phyllanthus (*8*), Reidia (*8*), Kirganelia (*8*), Emblica (*8*), Flueggia (*8*), Anti-desma (*8*), Hemicyclea (*8*), Glochidion (*8*), Daphniphyllum (*8*), Jatropha (*8*), Givotia (*8*), Sapium (*8*), Celtis, Gironniera, Trema, Ficus (bats), Laportea, Villebrunea, Globba, Curcuma, Hedychium, Zingiber, Costus, Elettaria, Alpinia, Schumannianthus, Phrynium, Musa (*7*, man), Hypoxis, Moleniera, Tacca (*6*), Asparagus, Smilax (ants), Dracaena, Disporum, Asparagopsis, Pinanga, Phoenix (bats), Calamus (bats), Kyllinga (*2*, cattle), Pycreus (*2*, cattle), Juncellus (*2*, cattle), Cyperus (*2*, cattle), Courtoisea (cattle), Eleocharis (*2*, cattle), Bulbostylis (*2*, cattle), Fuirena (*2*, cattle), Lipocarpha (*2*, cattle), Fimbristylis (*8*), Rhyncospora (*8*), Scleria (*8*), Eragrostis (*5*, *6*).

These genera are dispersed endozooically by cattle: Gynandropsis (man), Pimpinella, Carum, Anthocephalus (bats), Moniera, Striga (*6*), Echinochloa (*6*, bison), Dactyloctenium (ants), Eleusine (ants).

Other endozooic genera are: Polyalthia (bats), Viola (*1*), Waltheria, Buettneria, Hugonia, Erythroxylon, Reinwardtia, Zanthoxylum, Feronia (*8*), Aegle, Citrus (man), Balanites, Cipadessa, Azadirachta, Olax, Ximenia, Dichapetalum, Erythropalum, Strombosia, Opilia, Cansjera, Gomphandra, Mappia, Sarcostigma, Sageratia, Cissus, Cayratia, Leea, Nephelium, Schleichera (*6*), Sapindus, Buchanania, Spondias, Solenocarpus, Odina, Nothopegia, Semecarpus, Holigarna, Meliosma, Cassia (*6*), Entada (*6*), Indigofera (ants), Mundulea, Tephrosia, Millettia, Atylosia, Dunbaria, Wagatea, Tamarindus, Humboldtia, Xylia, Entada, Dichrostachys, Mimosa (goats, adhesion), Acacia (*6*), Albizzia, Terminalia (*3*), Careya, Gymnopetalum, Momordica, Bryonopsis (*6*), Coccinia, Melothria (rats), Breynia (*6*), Cactus (man), Alangium, Mastixia, Lonicera, Mussaenda, Mycetia, Chomelia, Randia, Gardenia, Plectronia Ixora (man), Pavetta, Maesa, Rapanea, Embelia, Sideroxylon (squirrels), Madhuca (bats), Isonandra, Palaquium, Symplocos (bats, rats), Ligustrum (*5*), Nyctanthes, Chilocarpus, Rauwolfia, Gardneria, Rivea, Cressa, Porana, Physalis (*6*, sea), Withania, Pedicularis (*6*), Premna, Gmelina, Vitex, Plantago (*5*, man), Lasiosiphon (*4*, elephants), Sarcococca, Cyclostemon (*8*), Beccaurea (*8*), Sauropus, Breynia, Aporosa, Putranjiva, Chrozophora, Mallotus (adhesion), Blachia, Adenochlaena, Artocarpus (torn into pieces by monkeys and pieces scattered), Debregaesia, Ophiopogon, Gloriosa, Sansevieria, Aloe, Scilla, Iphigenia, Commelina, Cyanotis, Caryota (monkeys), Pandanus (*6*, sea), Arisaema, Ariopsis, Amorphophallus, Anaphyllum, Pothos, Rhaphidophora Colocasia (man), Carex (*1*, *6*), Garnotia (*5*), Spodiopogon (*8*, insects), Capillipedium, Amphilophis, Coelachne (*8*), Tragus (*8*, ants).

B. c) 8. Epizooic dispersal, usually by adhesion.

The following genera are known to be epizooically dispersed by birds: Cerastium, Polycarpon, Paspalum (insects).

Other epizooic genera are: Dillenia (*6*, termites), Cardamine (ants), Polygala, Salomonia (ants), Drymaria (man), Garcinia (nibbling by monkeys), Ochrocarpus (nibbling by rats, *6*), Sida (*7*, ants), Pavonia, Abutilon, Kydia, Decaschistia, Cullenia, Melochia (man), Triumfetta (ants), Tribulus, Mangifera (nibbling by monkeys, man), Teramnus (*2*, *3*), Aeschynomene (*6*), Desmodium (*7*), Clitoria, Kalanchoe, Rotala (*6*), Ammannia (*6*), Nesaea (*6*), Jussieua (*6*, man), Heracleum (*3*, *6*), Adenostemma, Cyathocline, Vicoa, Siegesbeckia, Blainvillea, Moonia, Flaveria, Cotula, Wedelia (*6*), Spilanthes, Bidens, Echinops, Sphaeranthus, Senecio, Eclipta, Helianthus, Artemisia, Dicoma, Crepis, Erechthites, Plumbago, Anagallis (*7*), Sideroxylon (*7*, nibbling by squirrels), Paracaryum (*3*), Tournefortia, Heliotropium, Trichodesma, Cynoglossum, Rotula, Limnophyton (*6*), Moniera (*7*), Ilysanthes (*7*) Lindernia (*7*), Priva, Lippia (*7*), Ocimum, Orthosiphon, Acrocephalus, Geniosporum, Platystoma, Moschosma, Plectranthus, Coleus, Anisochilus, Hyptis, Lavandula, Pogostemon, Dysophylla, Anisomeles, Leucas (*5*, *6*), Teucrium, Boerhaavia, Pisonia, Amarantus, Cyathula, Pupalia, Alternanthera, Piper, Heckeria, Loranthus (seeds stick to birds' beaks), Elytranthe, Viscum, Mallotus, Sebastiana, Fleurya, Pouzolzia (*2*, *6*), Hydrilla (*6*), Lagarosiphon (*6*), Vallisneria (*6*), Blyxa (*6*), Ottelia (*6*), Amomum, Smilax (ants), Aneilema, Juncus (buoyant seedlings), Remusatia (adhesive bulbils), Lemna, Wolffia, Limnophyton, Eriocaulon (*3*, *6*) Fimbristylis (*7*), Rhyncospora (*7*), Scleria (*7*), Mariscus (*6*), Iseilema (*5*), Perotis (*5*, ants), Pseudoraphis (*6*), Spodiopogon (*7*, insects), Amphilophis, Vetiveria, Anthistiria, Apluda, Eremopogon, Schizachyrium, Andropogon, Hackelochloa, Ophiuros, Rottboellia, Brachiaria, Paspalum (insects, birds, adhesive), Paspalidium, Urochloa, Panicum (*5*), Cyrtococcum (*5*), Dactyloctenium (*7*, ants), Arundinella, Coelachne, Trachys, Tragus (*7*, ants), Sporobolus, Eleusine (*7*, cattle, ants), Pommereulla, Elytrophorus, Aeluropus, Chrysopogon, Dichanthium (*5*), Heteropogon, Themeda, Pseudanthistiria (*6*), Manisuris (*6*), Pseudechinolaena, Eriochloa, Cenchrus, Polypogon, Dinebra, Danthonia.

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RESTORATION OF THE ZOSTERA FACIATION AT CAPE ANN, MASSACHUSETTS

Following the almost complete eradication of eelgrass (*Zostera marina* L.) from the Atlantic Coast in 1931–32 as the result of a wasting disease epidemic, observations have been made on the status of this plant and its ecological relations at Cape Ann, Massachusetts, at various times during the past 16 years. An earlier report (Dexter, '44) summarized the situation in general and described the survival of a small area of eelgrass in Goose Cove at Cape Ann, with notes on the annual occurrences of small isolated patches and individual plants in the Annisquam River, to which Goose Cove is connected, through the year 1940. Subsequent reports (Dexter, '45, '46, '47a) described the gradual expansion of the Goose Cove remnant from a few acres in 1945 to a stand double its former size in 1946, to an expanded growth which filled three-fourths of the cove below low-water-line in 1947. Notes on small clumps and drifting fragments found elsewhere in the region were included. Addy and Aylward ('44), Cottam ('45), and Cottam and Addy ('47) have described the eelgrass situation of recent years at other points on the Massachusetts coast and elsewhere along the Atlantic seaboard.

In September, 1949, a resurvey of the entire Cape Ann area disclosed that eelgrass has not yet returned in significant quantity anywhere except in Goose Cove. In that location, however, a maximum stand of some 30 acres of healthy-appearing eelgrass has completely overgrown the subtidal bottom of the cove and the Zostera Faciation, long absent from the region, has been restored. (See figure 1.) While there was still evidence of persisting disease in the form of occasional brown-streaked leaves, a great many plants examined were free from such symptoms, and fragmentation of the leaves so commonly observed in past years was not in evidence. Most of the leaves were bright green and fully intact. Much of the reproduction was apparently derived from seeding, especially around the margin of the stand and on the formerly bare sediments. All available sediments were overgrown, including the mouth of a small brook which enters the cove and into which several individual plants had penetrated for several yards. Only the deep basin with a bottom of ledge and boulders at the sluiceway, kept clear of sediment by the swift current passing with the tidal flow and ebb, was free of eelgrass. Here the algae *Chondrus crispus* and *Laminaria* spp. replaced it on this rocky bottom.

On and among the blades of eelgrass was found for the first time an abundance of animal life. The English periwinkle (*Littorina littorea*) was in great abundance, peppering the leaves throughout the stand. Other mollusks collected were *L. saxatilis, L. obtusata, Lacuna vincta, Onoba aculeus, Gemma gemma,* and seed of *Mytilus edulis.* Crustaceans found in the eelgrass were *Idothea baltica* (isopod), an unidentified amphipod, and the shrimp *Crago septemspinosus.* A tube-building annelid *Spirorbis spirorbis* was attached to the leaves. Lobsters (*Homarus americanus*) and eels (*Anguilla bostoniensis*) have been captured in traps set in the cove. Fry of the salt-water minnow (*Fundulus heteroclitus*) and the three-spined stickleback (*Gasterosteus aculeatus*) were collected with a dip net. Feeding in the eelgrass beds at low tide were the green heron (*Butorides virescens*), great blue heron (*Ardea herodias*), and black-crowned night heron (*Nycticorax nycticorax*). At all tides the common Tern (*Sterna hirundo*) and the Kingfisher (*Megaceryle alcyon*) feed there. The shoreline of Goose Cove was ringed with a continuous thick heap of eelgrass wrack.

Surrounding the newly reconstituted Zostera community, in the sand-mud bar developed in the center of the cove and in the marginal mud flats, was found the typical Mya-Nereis pelagica Faciation. The following animals were collected there: *Mya arenaria, Macoma balthica, Solemya velum* (bivalves); *Nereis pelagica, Glycera dibranchiata, Lumbrinereis tenuis, Clymenella torquata* (annelids); and *Dolichoglossus kowalevskyi* (prochordate). Sandpipers, herring gulls, and crows feed there. At the present rate of sedimentation, this community can be expected to encroach upon the Zostera subtidal community and probably replace it in time, as well as crowd out much of the Balanus-Mytilus-Littorina community still found on the exposed ledges and boulders around the margin of the cove. The following organisms were found constituting the

FIG. 1. Goose Cove at low tide. Floating tops of eelgrass bed in foreground; sand-mud bar in right background.

latter: *Balanus balanoides* (rock barnacle); *Mytilus edulis* (blue mussel); *Littorina littorea, L. saxatilis, L. obtusata, Thais lapillus* (snails); *Ascophyllum nodosum, Fucus vesiculosus* (algae); *Gammarus locusta* (isopod); *Anurida maritima* (insect); *Acmaea testudinalis* (limpet); *Sertularia pumila* (hydroid); and *Spirorbis spirorbis.* Already three large patches of thatch grass, *Spartina alterniflora,* have invaded the top of the bar, and it has been established in many places along the shoreline so that the bivalve-annelid community of the sediments will in turn be replaced by a marsh community as explained in the writer's study of the marine communities of this tidal inlet (Dexter, '47b).

Goose Cove was nearly isolated from the main section of the Annisquam waterway by a road-fill constructed across the entrance to the cove in 1832. At that time two sluiceways were left open to permit tidal water to continue to flow into the cove. In 1919–20 the south sluiceway was closed. (See U. S. C. and G. S. map 233: Gloucester Harbor and Annisquam River.) This partial isolation may have been responsible for the conditions which permitted eelgrass to persist at a time when the species disappeared in other sections of the region. The road-fill certainly is the cause of the rapid sedimentation and succession which have taken place in recent years.

Elsewhere on Cape Ann, the eelgrass situation was found to be about the same as observed in 1947. The channel entrance to Goose Cove on the west side of the road-fill was about 25 per cent covered with eelgrass, although this growth was not as healthy appearing as within the cove. Mr. Herbert Montgomery found two small patches growing in nearby Lobster Cove. Occasional fragments were observed floating in the Annisquam River in the vicinity of Goose Cove, and probably came from that source. Mr. Harold Geary also observed floating fragments at various points in the Annisquam River. No living patches or plants were found in the main river channel however. At Wingaersheek Beach, facing Ipswich Bay at the northern entrance to the Annisquam River, many scattered seedlings and several young patches of eelgrass up to a square foot in area were found growing in the sand along spring-low-water-line. Fragments of detached but fresh leaves were found on the beaches at Hodgkins Cove and Plum Cove, also facing on Ipswich Bay. Beyond that point, however, no evidence of eelgrass was found growing in the shallow water or strewn along the windrows with the exception of small, dried fragments rarely found in several places. Along the eastern shores of Cape Ann, facing the Atlantic Ocean, no signs of eelgrass were detected anywhere. In Gloucester Harbor, however, at the southern end of the Annisquam tidal inlet, many fragments of fresh blades floating in the water and strewn on the shores and beaches indicate that Zostera is at least holding its own in the harbor as reported for 1947, but probably is not present in any great quantity.

At Goose Cove, at least, the Zostera Faciation has been fully restored, although the return of eelgrass in other sections of Cape Ann has not yet made much progress.

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FENCING NATURAL AREAS

At the University of Illinois, biologists have had experience with several types of fence in part intended to permit free movement of small game birds and mammals and at the same time make entrance by humans as uncomfortable as possible. Some simple experimental work was done. Common woven wire fencing was in part installed with the small meshes at the bottom, and in part with the wide meshes at the bottom. Bird and mammal tracks along the fence were examined carefully when there was good tracking snow. The quail and rabbits went directly through the fence with the large meshes at the bottom, but those that came to the fence with the narrow meshes at the bottom moved along some distance one way or the other, and sometimes back and forth, before they squeezed their bodies through small openings. This tends to confirm statements that have been made by some wildlife managers to the effect that areas fenced with small mesh fencing, such as Cyclone Fence, have less game animals than similar areas unfenced and with unauthorized hunting. It is assumed that game animals which get out through difficult fences do not take the trouble to return. As to size of meshes, Dr. R. E. Yeatter of the Illinois Natural History Survey states that raccoons entered boxes with $7'' \times 7''$ openings, but this is smaller than the usual estimate. If, with longer experience, this proves large enough for large individuals, it will be better than the larger meshes because it will exclude the larger dogs, but until then probably $7'' \times 14''$ openings are a safer minimum.

In 1939 a fence was built around the 65-acre tract. Thirty-one-inch woven wire fencing was placed on alternating steel and creosoted wooden posts. There were three strands of barbed wire above the fencing and three strands on extension arms projecting outward. These arms were about 18 inches long and projected at an angle of 45 degrees. This fence was not very successful in keeping out trespassers.

In 1946 a fence similar to the one figured was built around a nominal 79-acre tract.[1] Farm fence materials were used except for rings and mill work. This fence does not differ in appearance from the one shown in figure 1 except in (a) the absence of the six rings above the double gate, (b) the lack of the inner bottom wire on the rings, and (c) in the use of lower woven wire. In the following discussion the existing fence is described, its defects pointed out, and proposed improvements elaborated. Many of these are concerned with structural defects in the existing fence.

It consisted of 31-inch high woven wire fencing with the wide meshes at the bottom placed on steel posts (angle type). Eighteen-inch rings were fastened on the posts (angle type $1\frac{1}{4}'' \times 1\frac{1}{4}'' \times \frac{3}{16}''$) immediately above the top of the 31-inch woven fencing. The rings bore four strands of barbed wire, three on the outside and one on the inside. (See fig. 1A.) At the corners, elliptical rings (fig. 1, C and E) were bolted on the corner posts (angle type $3'' \times 3'' \times \frac{1}{4}''$) at an angle of 45 degrees between the two line fences on the inside of the corner, or 135 degrees from the two line fences on the outside. These elliptical rings were of such size as to project the same distance (9 inches) as the circular rings on the line posts. Regular farm angle posts were used.

There are a number of structural and practical difficulties, which include weakness of the

[1] A nominal 80 acres less a nominal 1 acre school site.

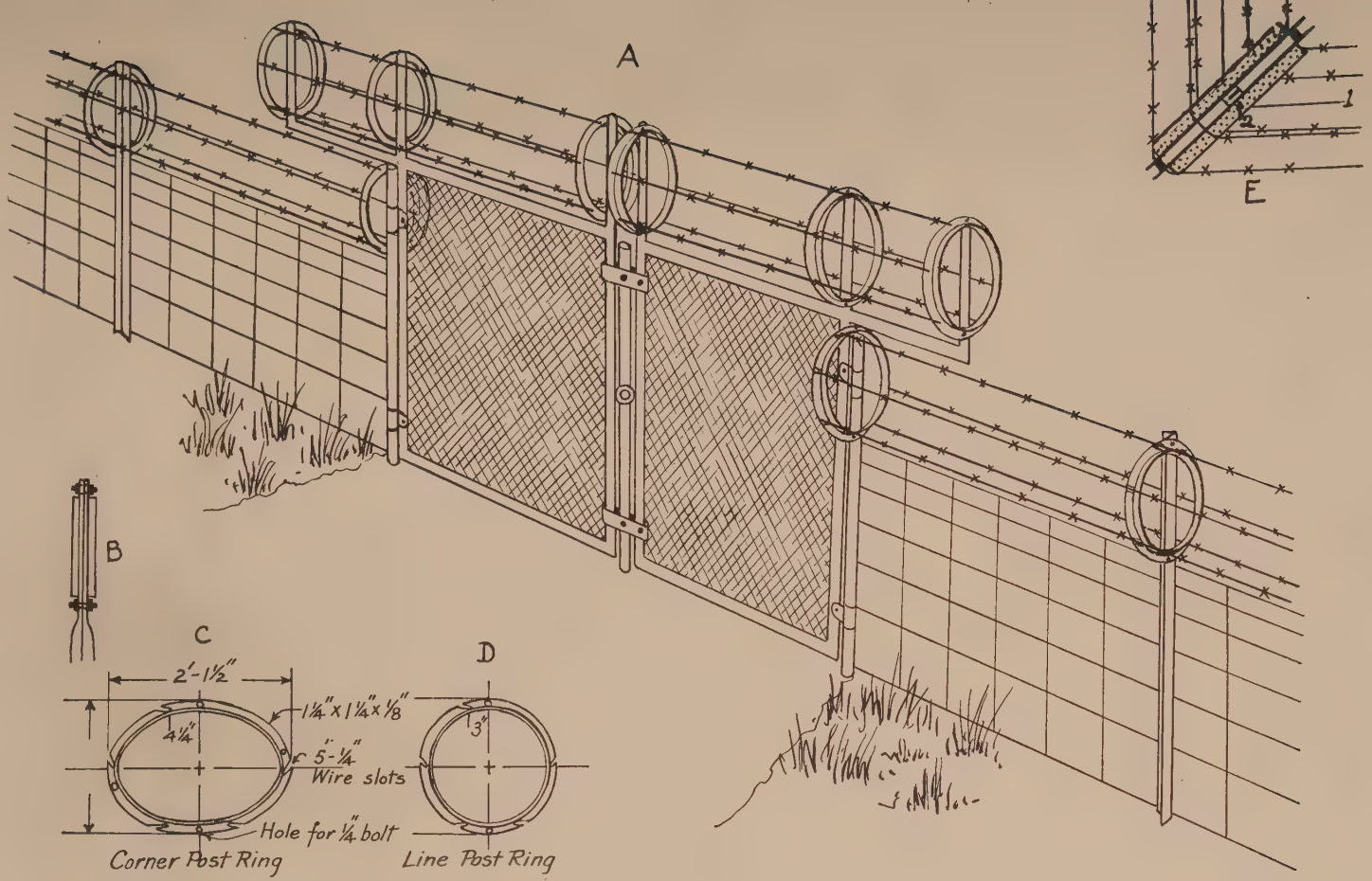

FIG. 1. A, shows a perspective view of a double gate and two full panels of fence; the gate post braces and heavy concrete in which the gate posts and braces must be set, are not shown. B to E are details. B shows the top 18 inches of a corner angle post rolled together so that the two sides stand at 45 degrees to the original sides of the lower half of the post. C and D show an elliptical corner ring and a round line ring with five barbed wire slots. E shows the two elliptical rings with double top of the post at their center between them, seen from above with five barbed wires and spacer washers. 1 is the top of the woven wire fencing. 2 is the corner post top.

corner post and ring, too great lengths without braced panels, and too great ease of climbing. Persons wishing to enter the area are able to do so by lying flat on top of the woven wire fencing and throwing one leg over. The 31-inch height is average leg length. The ease of this type of fence climbing was increased by the omission of inner bottom wire from the rings. One of two persons can pull the single wire upward and outward while the other one puts first one foot and then the other over; in one case the wire was removed from the slot and the No. 12 wire which held it was removed. The gates provided with this fence merely have vertical end pieces extending above the top of the woven wire, bearing three strands of barbed wire. The gates have frequently been climbed as shown by the marks on the paint and reports of persons who forgot their keys.

A modification of the fence described above is proposed to eliminate these difficulties. First of all, a 39-inch high woven wire fencing, which is about 8 or 9 inches higher than the average leg length, should be used. The inside wire on the bottom of the rings adds a large measure of difficulty for the climber while keeping one foot or the other on the ground. To prevent removal of the wires from the slots, No. 9 wire should be used to tie them in. The difficulty at the gates can be remedied by putting rings on the top of the gates (fig. 1A). The woven wire covered frames of the gate are 57 inches high. Above these, three rings should be installed upon each half of a double gate and four rings on a single gate. These rings would be borne on a frame which projects 24 inches over the top of the fence, thus rendering the climbing at the gates impracticable. Care must be used to eliminate foot rest on the commercial double gate locking device and to see that the rings on the two halves are less than 2 inches apart when the gates are closed. It may be necessary to have these rings bent slightly.

Some manufacturers have listed rings in the recent past. The rings used were based upon samples taken from a 9-ft. fence built by the University in the early 1880's. They were tried out on a temporary 1320-ft. fence section 46 inches high. The omission of the inner lower barbed wire on the new rings was due to a clerical error in ordering the new fence. Triangles provided for stock fences were rejected by a committee as inadequate for a low fence.

In order to remedy the structural weaknesses encountered, it is proposed to have the two sides of the corner angle posts rolled together (fig. 1, B and E) and to use two elliptical rings, one with the flange to the right and one with the flange to the left, bolted to heavier posts and bolted together with a spacing washer of the same thickness as the corner posts. Every 298 or 330 feet there should be a braced panel of fence or a heavy braced post with double circular rings with right and left flanges, bolted together like the double corner ring. The post or posts could be round tabular structures rolled flat for 18 inches (dia. 2½").

The objective in the construction of such fencing is to keep costs low and to permit free movement of birds and mammals. At present the fence most commonly used to keep trespassers out is a 6-ft. chain link fence (2" mesh) with complete panel frames, all posts set in concrete and oblique extension arms which make the total height 7 ft. One mile with two double gates now costs $2.40 per foot installed; 300 ft. with two gates costs $3.00 per foot installed. Cyclone is a common brand made by U. S. Steel, but at least three companies make essentially the same fence. The fence described will cost 65¢ to 70¢ per foot by the mile with two double gates. The fence companies advise that it will be cheapest to have one of them make the fence described and install it. Stock gates can be easily modified to carry the high rings at the time of manufacture. All materials should be heavily galvanized after milling. Commercial so-called man-proof fence not only does not permit the free movement of animals, but can be climbed at the gates or even elsewhere, especially by small boys who can get their toes into the meshes of the woven fencing.

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THE COMPOSITION OF A REMNANT OF WHITE PINE FOREST IN THE LAKE STATES[1]

During the summer of 1946 the writer had several opportunities to examine small stands of white pine which appeared to be completely undisturbed. These areas average about one acre in size and are relatively inaccessible. They are intact today primarily because the lumbermen of the period 1880–1910 could not reach them readily.

One such area located on the Gillen Refuge

[1] The writer wishes to express his appreciation for the timely suggestions of Drs. Cottam and Curtis and Mssr. Brown and McIntosh of the University of Wisconsin.

TABLE I. *Composition of the arboreal layers of the Plum Lake pine stand**

Species	Density Trees per acre		Per cent density	Per cent dominance	Per cent frequency	DFD index
	Over 1" d.b.h.	Over 12" d.b.h.				
Pinus Strobus	51	41	6.25	40.5	75	121.75
Betula papyrifera	91	50	11.3	24.5	75	110.8
Tsuga canadensis	485	30	60	30.3	100	190.3
Acer saccharum	111	—	13.8	2.5	75	91.3
Abies balsamea	51	—	6.25	1.3	50	57.55
Thuja occidentalis	10	—	1.2	.38	25	26.58
Betula lutea	10	—	1.2	.38	25	26.58
Total all species	809	121	Calculated basal area 365.2 sq. ft. per acre			

* Percentages given are based on all trees present over 1 inch d.b.h.
Total area sampled is 400 sq. meters or 0.098 acres. The sample included 80 trees with a basal area of 36.1 square feet.

along the Wisconsin-Michigan state line, just east of Plum Lake, Vilas County (Section 9, Town. 43 N, Range 8 E), was studied in some detail. The writer wishes to express his sincere thanks to Rev. J. J. Reddington of Notre Dame University for assistance in making this study. This particular stand occupies a peninsula extending into a spruce-cedar swamp and owes its existence to its island-like position. The swamp protected the stand from cutting and from the ensuing fires which burned to the edge of the swamp in the slashings to the north and east.

Four quadrats, each 100 square meters in area, were used to sample the arboreal composition of this "pine island." The results are presented in tables I and II.

The basal area computed for this stand is high, 365.2 square feet, in comparison to 269.2 square feet calculated for a nearby virgin hardwood stand. The large white pines and the smaller but sizeable white birch are largely responsible for this high figure to which the dense stand of medium and small hemlocks also contributes.

The ground cover is sparse both in species and numbers. Herbaceous species were sampled on four 1×4 meter quadrats. *Maianthemum canadense* is the most common species present with a density of 7 plants per quadrat. *Lycopodium obscurum* is next with 4 plants per quadrat. *Clintonia borealis* follows with a density of 1 plant per quadrat while *Monotropa uniflora* has a density of 0.5 plants per quadrat. Species represented by only one individual in the herbaceous quadrats (i.e. density of 0.25) include *Lycopodium annotinum, Dryopteris spinulosa, Schizachne purpurascens, Trientalis borealis* and *Chimaphila umbellata. Coptis trifolia, Cornus canadensis* and *Viola* spp. were observed in the stand.

Tree reproduction is very limited, consisting primarily of sugar maple with a little fir and hemlock. The calculated density of sugar maple reproduction, 1846 seedlings per acre, is approximately $\frac{1}{16}$ the density of sugar maple seedlings in the adjoining virgin hardwood forest. All of the twelve hemlock seedlings recorded were growing on well rotted logs in one quadrat. Only a few isolated seedlings of

TABLE II. *Diameter distribution of tress.**

Species	1–3.9 inches	4–7.9 inches	8–11.9 inches	12–19.9 inches	Over 20 inches
Pinus Strobus			1	1	3
Betula papyrifera			4	5	
Tsuga canadensis	13	25	7	3	
Acer saccharum	8	2	1		
Abies balsamea	1	4			
Betula lutea		1			
Thuja occidentalis		1			
Total	22	33	13	9	3
Trees per acre	223	333	132	91	30

* Trees recorded on four 100 square meter quadrats.

yellow birch, white pine and white birch were observed in the stand.

The large pines, most of them hollow with damaged or irregular tops, are undoubtedly very old. One tree just outside a quadrat measured 36 inches d.b.h. while another nearby was 40 inches. In 1941 a section was taken, at the first sound point about 35 feet up the trunk, from a similar pine which had been windthrown. This section was given by the late Martin Gillen to Dr. John T. Curtis of the Botany Department of the University of Wisconsin. Counted by the writer, it showed 341 rings in a 30-inch diameter. The rate of growth during the first hundred years was very slow, less than half that during the next 150 years, while the rate during the last 80 years of growth was again slow. The age of the tree was at least 380 years at the time that it was cut. It is probable that the larger pines recorded in the stand, 26, 27, 31, 36, and 40 inches d.b.h. respectively, are of approximately the same age, now about 390 years.

The white birch is also old and similarly shows signs of decadence with numerous windfalls and dead stubs present in the area in addition to the standing trees. It was not possible to obtain satisfactory cores from the birches, which in all likelihood became established at the same time as the hemlock and the younger pines. Evidence from cores indicates that the hemlocks and pines became established 160 to 175 years ago. That white cedar entered the stand at that time is evidenced by a 14-inch tree and several others 8 to 10 inches.

The history of this stand would appear to begin with the establishment of white pine following some early catastrophe. Several hundred years later some lesser disturbance occurred which provided the bare mineral soil and the light necessary for the establishment of hemlock, white birch, cedar and the smaller pine. In the future, if the stand remains undisturbed, sugar maple will gradually gain in importance as the old white birch dies and the aging pine succumbs to the elements. Hemlock will probably be a very important part of the cover for several hundred years and some of the trees may reach great size. The presence of the younger 8- and 16-inch pines should insure a seed source so that pine will probably continue as a component even without major disturbance, establishing itself occasionally as in the past along the steep sandy slopes that mark the edge of the cedar swamp. More pine reproduction would perhaps be evident today were it not for the activities of the red squirrels whose "kitchen middens," of chewed cones, cone scales and twigs are to be seen on every large fallen log. If the stand is opened up by heavy windfall conditions may become favorable for basswood, yellow birch, ash and elm to seed in from the neighboring hardwood stand. On the other hand severe disturbance, in the fall of a good seed year, may result in abundant pine reproduction.

This brief report is made to place on record further details concerning the composition of the pine forest. The very small area of such residual patches as this one makes any statistical analysis subject to doubt and calls for a study of as many stands as can be found. The need for further studies is imperative both to further our understanding of the white pine complex and to provide a basis for studies on the rate and nature of the process of natural revegetation.

Since the data for this paper were obtained, the importance of wind as an agent of mortality in the forest has been curtly underlined. On October 10, 1949, winds of hurricane force were recorded at many points in Wisconsin, Minnesota and neighboring states. During this storm approximately 5,000,000 board feet of timber was lost from the only remaining virgin hardwood stand along the Flambeau River and about half of the virgin red and white pine stand at Trout Lake, Wisconsin, was destroyed (personal communication, J. T. Curtis). It is probable that the stand discussed in this paper was destroyed or seriously damaged, making the description presented here one of historical record.

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WET SEASONS IN THE UNITED STATES: HOW WET AND HOW FREQUENT

Wet seasons are of such profound significance that information is widely welcome on the extent and frequency of excessive precipitation. The Weather Bureau issued in 1943 several tables which permit the construction of maps which make more widely available valuable information on these topics.

The accompanying 16 maps show for each of the four seasons (spring, summer, autumn and winter): 1) how much precipitation occurs in a relatively wet season, that is, in one so wet that only one season in five is wetter; 2) the most precipitation received in 52 years; 3) the approximate percentage of the seasons which re-

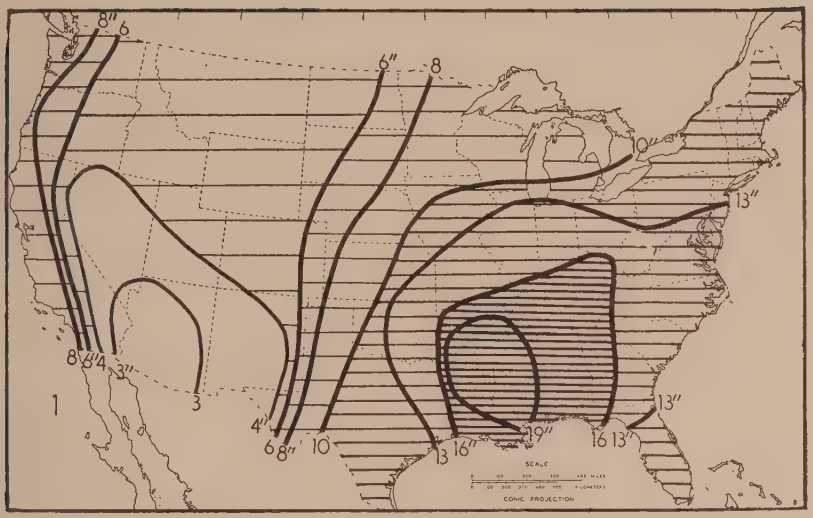

FIG. 1. Inches of precipitation received in a relatively wet spring (⅘ receive less, ⅕ receive more).

ceive a seasonal total of more than 15 inches for the three months; and 4) the percentage of the seasons which receive a total of more than 20 inches, an amount normally exceeded by only a small fraction of the earth.

These Weather Bureau tables are based on state averages, and hence the isolines on the present maps are only approximate. (They have been drawn, however, with the aid of more detailed maps by Kincer ('41).) As small areas therein often receive considerably more precipitation than the average of a sizable area, the present maps are distinctly conservative. The third map for each season, the one of the approximate percentage of the seasons in which more than 15 inches of precipitation is received, is only approximate, because the available data are inadequate. From these data, two sets of maps have been made, one based on the seasonal averages of the percentage frequencies of each of the three months which receive more than 5 inches per month Kincer ('43), and the other

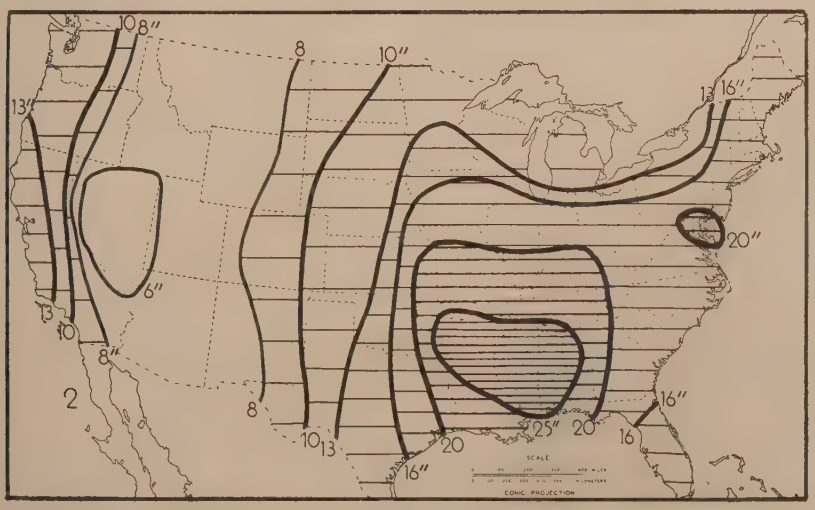

FIG. 2. Inches of precipitation received in the wettest spring of 52 years.

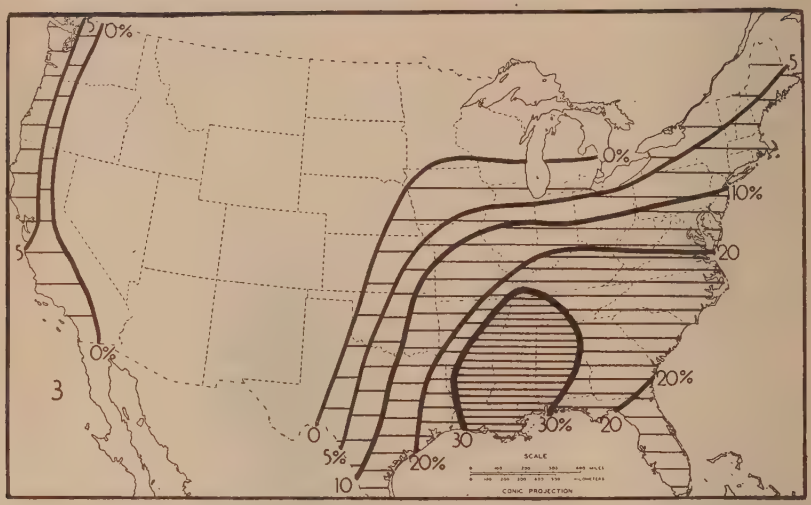

FIG. 3. Percentages of the springs which receive more than 15 inches of precipitation.

based on the seasonal totals in the 10 wettest seasons of 1886–1938. The first of these preliminary maps gives a frequency which is too high, because one of the three months of a wet season commonly is dry enough to offset partly the two other months. The second of these preliminary maps gives percentages which are too low, as the maximum possible from the available data is 20 per cent, when in fact some frequencies run as high as 80 per cent. The frequency map here given (the third for each season) is intermediate between these unpublished frequency maps.

The percentage frequencies of various totals of precipitation for each of the 12 months are mapped and briefly discussed elsewhere (Visher, '44b). A discussion of the dry seasons comparable to the present one appeared in the July 1949 issue of ECOLOGY (Visher, '49).

.. WET SPRINGS

Figure 1 shows that in four-fifths of the years the total spring precipitation received is less than 10 inches in more than half of the country, but that in a sizable southeastern area the total ex-

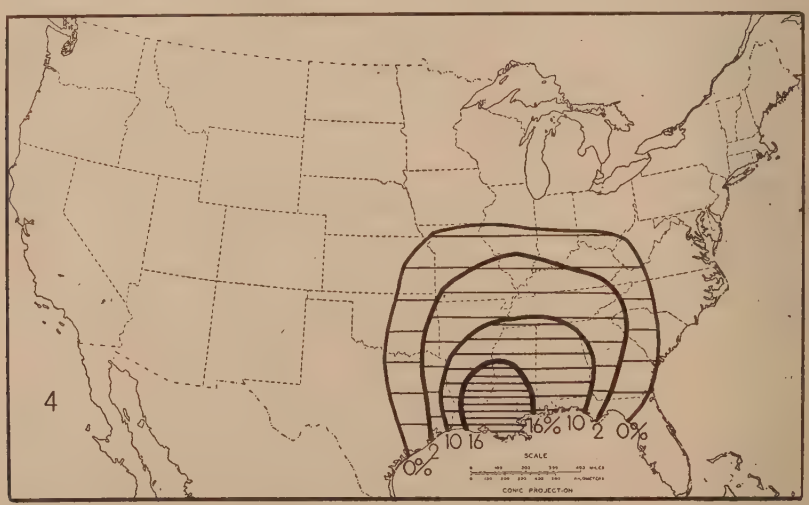

FIG. 4. Percentages of the springs which receive more than 20 inches of precipitation.

ceeds 16 inches, in part of it, more than 19 inches. Conversely, in a large southwestern area, less than one spring in five receives as much as 4 inches of precipitation. Arizona, the driest state in this category, receives an average of 2.4 inches; a large northwestern interior region receives 4 to 6 inches, and most of the norhteastern quarter of the country receives from 9 to 15 inches.

Figure 2 shows that once in about a half century (once in 52 years) the total precipitation in spring is in excess of 16 inches in nearly a third of the country and more than 25 inches in more than 100,000 square miles between the Gulf of Mexico and the Ozarks. Arkansas has had a state spring average of 26.7 inches; Nevada, the most arid state, has had an average of 5.5 inches. The wettest spring in Michigan had less precipitation than did Nebraska (11.1 *vs.* 11.5). (The dates of the three wettest springs for large sections of the country are given in table 1.)

Figure 3 shows that throughout more than half of the country the spring season nearly always receives less than 15 inches, but that in a large southeastern area at least one spring in five receives more than 15 inches. In the lower Mississippi Valley such wet springs occur in nearly one-third of the years. Indeed, during the average or normal spring, Louisiana receives 14.9 inches as a state average, Arkansas 14.3, Alabama 14.2, Tennessee 14.0, Georgia 13.3. (These data are from the state tables in "Climate and Man" (Kincer, '41).)

Figure 4 shows that in only about one-fifth of the country are spring totals in excess of 20 inches received. In an area centering near Baton Rouge, Louisiana, however, such very wet springs normally occur one year in six or oftener. (Louisiana and Mississippi had 20 inch state average totals eight times in 52 years.)

Figures 1–4 make clear that large amounts of precipitation occur in spring in the Southeast, especially in the western part of that region, near the lower Mississippi River. The Pacific Coast belt occasionally receives 10 inches in this quarter-year, but in part of the Deep South twice that amount is received in about one-sixth of the springs, and more than 25 inches is occasionally received.

Very heavy rainfall in spring interferes, of

TABLE I. *The wettest seasons of 1886–1940 by regions*

	The three wettest in decreasing order	Percentage of the normal precipitation received in wettest season	Average of 3 wettest
Spring			
Northeast	1901, 1940, 1929	150	143
Southeast	1912, 1929, 1922	165	160
Midwest	1927, 1892, 1922	157	150
Great Plains	1892, 1927, 1935	160	150
Mountain States	1905, 1906, 1938	150	148
Pacific States	1896, 1938, 1893	150	145
Summer			
Northeast	1903, 1928, 1915	150	142
Southeast	1906, 1928, 1916	150	146
Midwest	1926, 1902, 1915	175	158
Great Plains	1915, 1928, 1905	160	143
Mountain States	1923, 1913, 1925	160	153
Pacific States	1888, 1937, 1912	230	210
Autumn			
Northeast	1907, 1888, 1927	160	152
Southeast	1932, 1888, 1935	155	150
Midwest	1919, 1925, 1926	170	152
Great Plains	1923, 1919, 1926	160	150
Mountain States	1940, 1919, 1925	155	150
Pacific States	1909, 1925, 1935	170	153
Winter*			
Northeast	1914, 1890, 1936	150	148
Southeast	1936, 1935, 1902	145	140
Midwest	1936, 1915, 1889	180	162
Great Plains	1914, 1918, 1902	175	153
Mountain States	1889, 1915, 1906	175	160
Pacific States	1886, 1939, 1935	200	155

* December of the year given and the two following months.

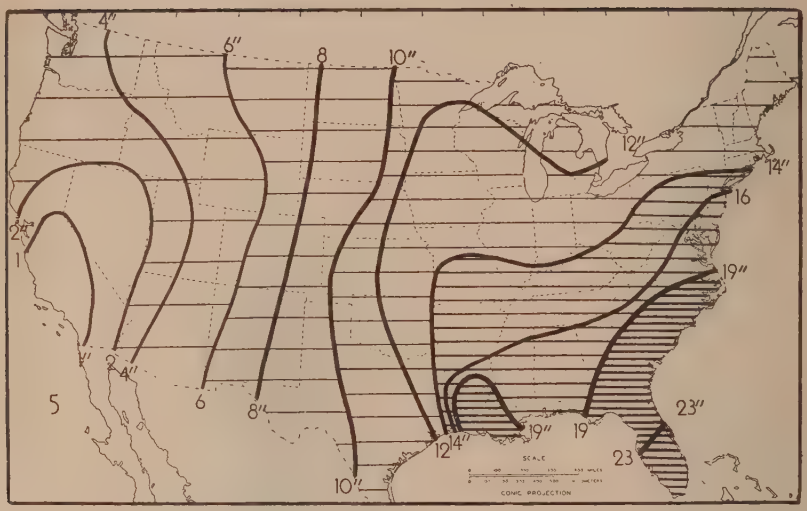

FIG. 5. Inches of rainfall received in a relatively wet summer (only 1/5 receive more rain).

course, with soil cultivation, sharply increases soil erosion on recently cultivated slopes, causes considerable flood damage, and helps to explain the low per capita income. The fact that the area which has the greatest amount of spring rainfall, and most frequently has very wet springs, contains a relatively large proportion of negroes is probably not merely coincidental. (Mississippi, Alabama and Georgia each had in 1940 approximately a million negroes and Louisiana 850,000.)

WET SUMMERS

Figure 5 shows that in a relatively wet summer, one so wet that only one-fifth receive more rainfall, only the Southwest receives less than 3 inches while more than 19 inches is received in a considerable southeastern and Louisiana area. Florida receives an average of 23 inches. California's average in such a relatively wet summer is only 0.8 inch. Most of the country's northeastern quarter receives 12 to 16 inches.

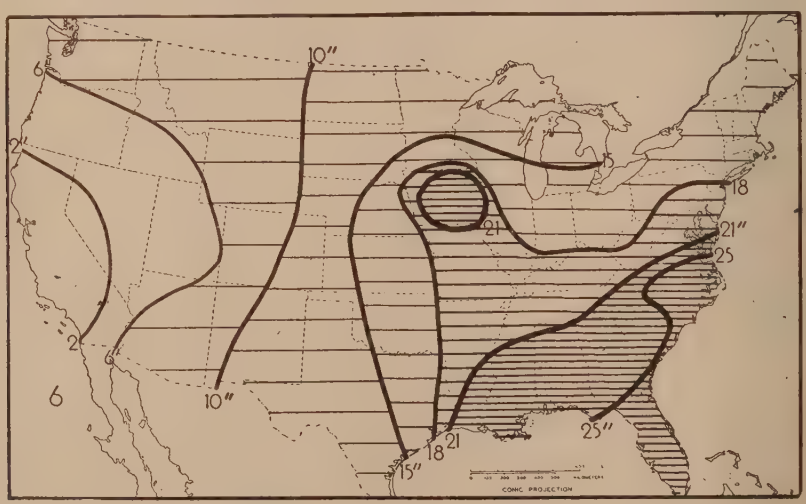

FIG. 6. Inches of rainfall received in the wettest summer of 52 years.

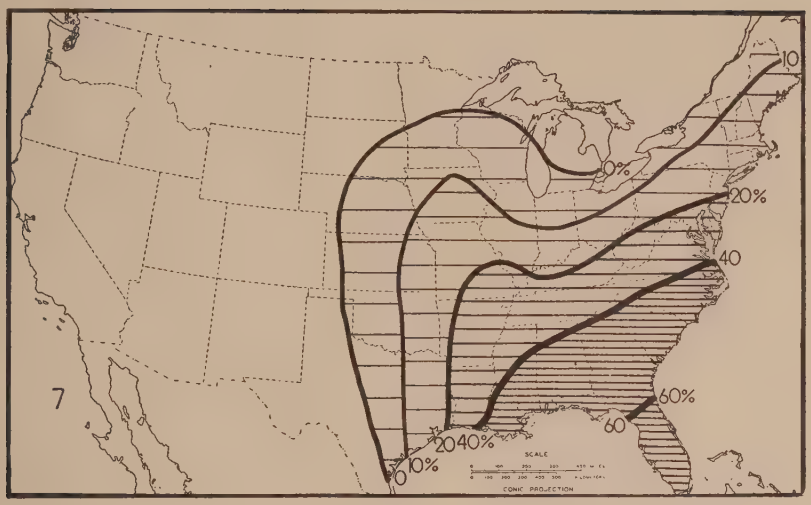

FIG. 7. Percentages of the summers which receive more than 15 inches.

Comparison with map 1 shows that the total received in a relatively wet summer is considerably greater than in a relatively wet spring, except in the western third of the country and in an area centering in Tennessee.

Figure 6 shows that in the wettest summer of 52 years totals in excess of 21 inches have occurred in the Southeast and in Iowa, but that California never has had an average of one-tenth that much summer rain. The totals shown in figures 5 and 6 are rather surprisingly large east of the Great Plains. They prove that the Southeast is sometimes very rainy in summer, which, in connection with the high average temperature which then prevails, produces considerable enervation. Florida has had a state average of 27.0 inches, North Carolina one of 25.8, South Carolina 24.2 and Alabama 23.6. At the other extreme, the wettest summer in California had a state average of only 1.5 inches and Nevada one of 4.0. More than half of the country has had a summer with more than 14 inches, enough, if well distributed, to support an abundant harvest. (For the dates of the wettest summers see table 1.)

Figure 7 shows that summer rainfall totals in

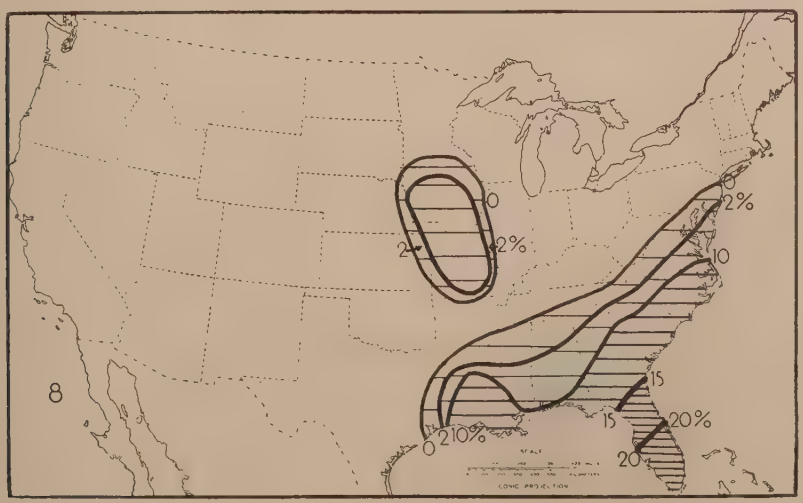

FIG. 8. Percentages of the summers which receive more than 20 inches.

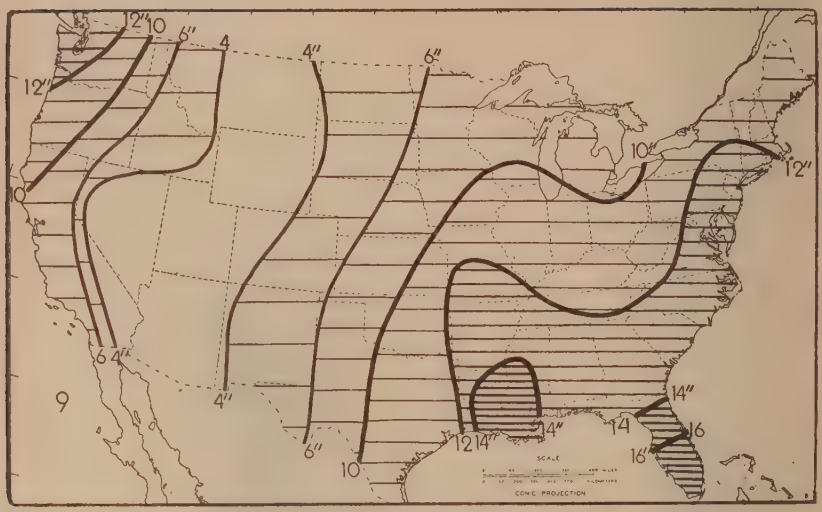

FIG. 9. Inches of rainfall received in a relatively wet autumn (only 1/5 receive more).

excess of 15 inches are lacking in the western half of the country and also near Lakes Superior and Huron, but that such wet summers occur in one year in five or oftener in the Southeast. In Florida more than half the summers are that wet. The very wet summers of Florida help explain its low soil fertility, and its slight appeal as a summer resort, despite the fact that the temperatures are less high than in the northern interior, where the summer days are longer, and where there are no cooling sea breezes.

Figure 8 shows that summer rainfalls in excess of 20 inches occur in the Southeast, where such very wet summers occur in more than one-fifth of the years in Florida, and once a half century along a line extending from New Jersey to Louisiana. In Missouri and Iowa, also, summers with 20 inches of rainfall occur about once in fifty years.

Comparison of figures 4 and 8 shows that very wet summers are scarcely more widespread than are very wet springs, but that their distribution

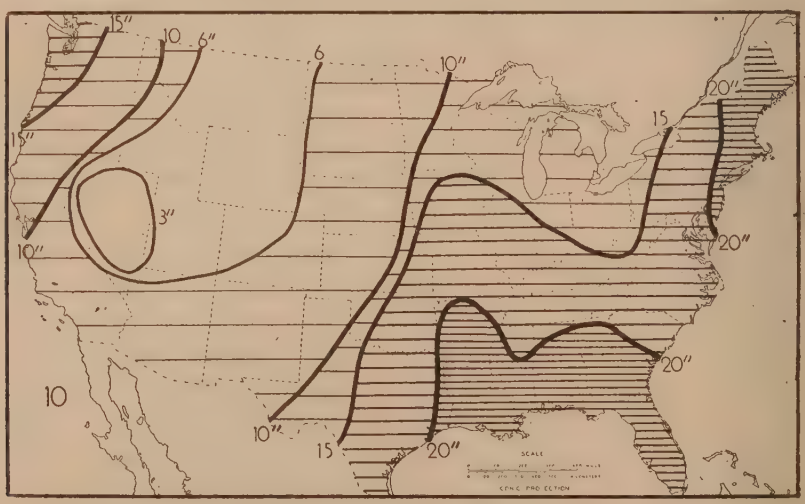

FIG. 10. Inches of rainfall received in the wettest autumn of 52 years.

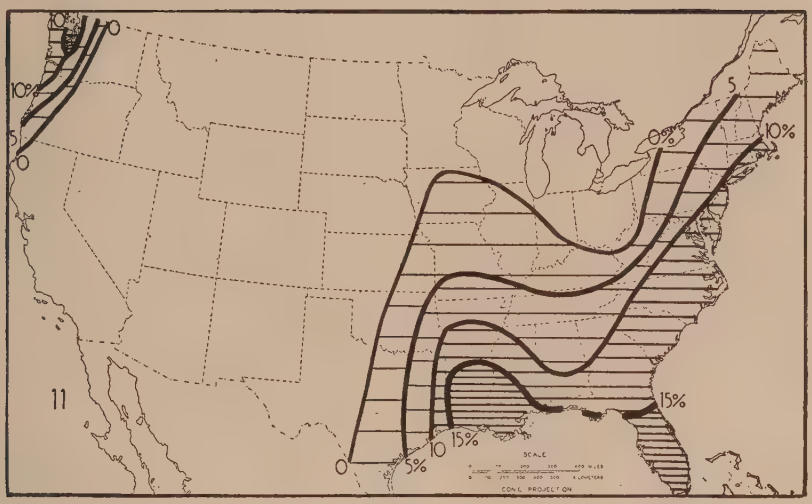

FIG. 11. Percentage of the autumns which receive more than 15 inches.

is different; the especially wet summers are found to the southeast, east and northwest of the area of very wet springs.

WET AUTUMNS

Figure 9 shows that in a relatively wet autumn (four-fifths receive less rain) considerably less precipitation is received than in either summer or spring; except chiefly on the Pacific Coast. In a large southeastern region and in a small northwestern one, the total is over 12 inches, however. Nevada is the driest state in this category, with an average of only 2.2 inches. Florida is the wettest state, with 16.3 inches, which, however, is only about two-thirds of its summer total.

In the wettest autumn of 52 years (fig. 10), the totals are also less than in spring or summer except on the Pacific Coast and in the Northeast. Totals between 20 and 22 inches occur in the Deep South and in New England and New Jersey. Only Nevada has received less than 3 inches in its wettest autumn. Louisiana has the highest total, 22 inches, Alabama 21. In most

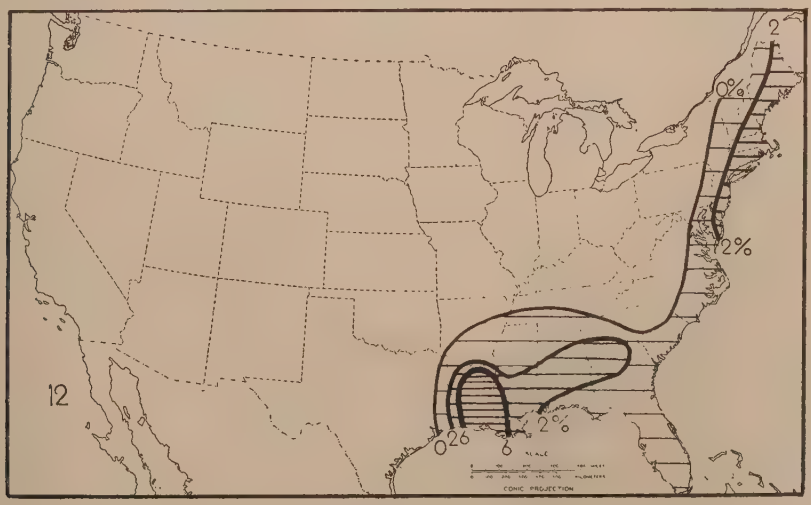

FIG. 12. Percentage of the autumns which receive more than 20 inches.

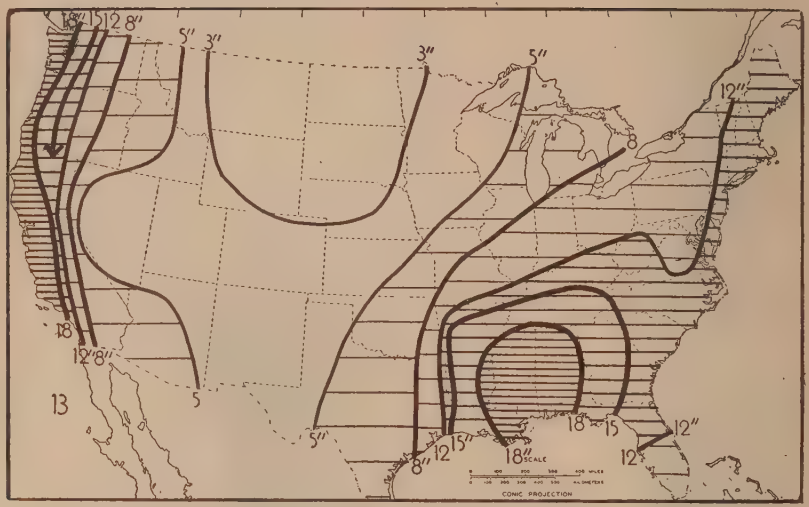

FIG. 13. Inches of precipitation received in a relatively wet winter (only 1/5 receive more).

of the East, the totals are 14–21 inches, while in a large west-central region they are 5–7 inches. (For the dates of the wettest autumns see table 1.)

Figure 11 shows the relative frequency of autumns which received a total of 15 inches or more of precipitation. It reveals that such wet falls occur most often in Louisiana and Florida (each with an average of 18 per cent), but that from Massachusetts to Texas on and near the coast one autumn in ten is this wet.

Figure 12 shows that 20 inches of autumn precipitation is lacking for a state average in nearly all of the states. However, once a half century such a total has occurred in New England, New Jersey, Georgia and Alabama, and 3 times in Louisiana.

WET WINTERS

Wet winters are distinctly more frequent than are wet autumns near the Pacific coast and also in the Southeast.

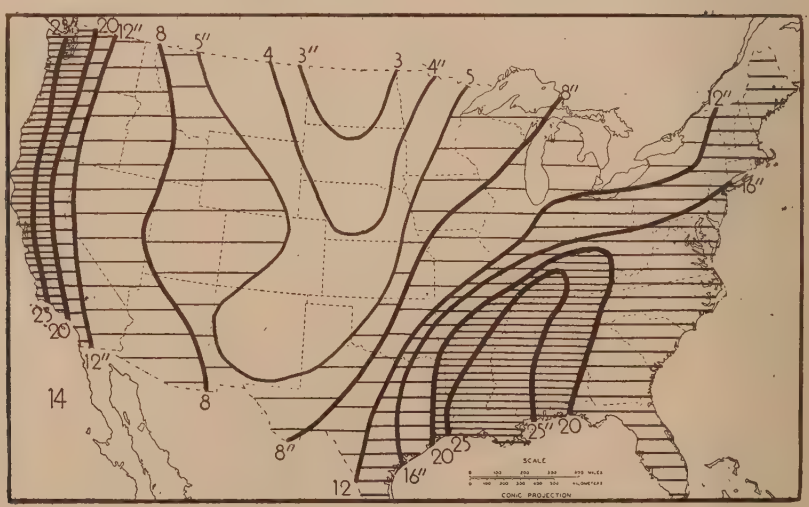

FIG. 14. Inches of precipitation received in the wettest winter of 52 years.

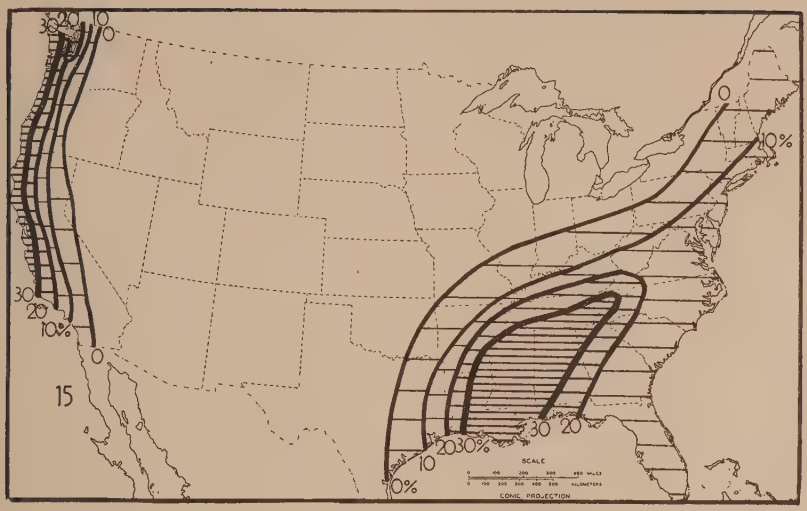

FIG. 15. Percentage of the winters which receive more than 15 inches.

In a relatively wet winter (fig. 13) two sizable areas receive more than 18 inches, namely along the Pacific coast and in Mississippi-Alabama. Somewhat more than 12 inches is received in the wettest one-fifth of the winters in New England and in Florida. By contrast, even in a wet winter a large north-central area receives less than 3 inches, North Dakota only 2.0.

In the wettest winter of 52 years the totals range (fig. 14) from 2.7 inches in the driest state (North Dakota) to 28.5 inches, or almost 11 times as much, in the wettest state (Mississippi). Louisiana got 25.5 inches and four states near these two got almost 25 inches. (For the dates of the wettest winters see table 1.)

Winters during which 15 inches or more of precipitation is received are lacking, according to figure 15, in most of the country, but occur in more than one-tenth of the years in sizable southeastern area and along the Pacific Coast. Such wet winters occur in more than 30 per cent of the years in a narrow Pacific belt and in an area centering in Mississippi. Indeed in Mississippi, the average winter total is 15.3 inches. Other states with high winter averages

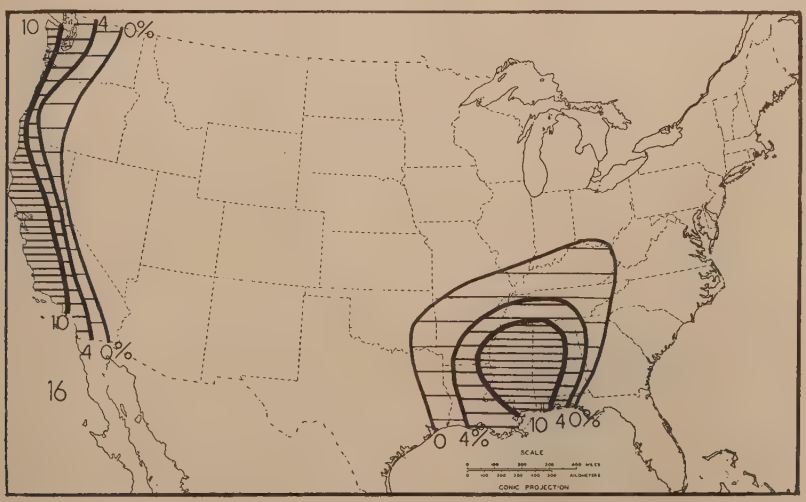

FIG. 16. Percentage of the winters which receive more than 20 inches.

are Louisiana 14.5, Washington 14.4, Tennessee 13.7, Georgia 13.3, California 13.1 and Arkansas 12.0.

The final map (fig. 16) shows that winter totals of 20 inches of precipitation are unknown, as state averages, except near the Pacific Coast and in a south-central area. They are distinctly less widespread and frequent than are totals of 15 inches (fig. 15). However 20 inch totals occur in about one-tenth of the winters in Mississippi and on the Pacific Coast. The exceptionally rainy parts of western Washington and Oregon normally receive winter totals in excess of 30 inches. (Five stations in western Washington and one in western Oregon normally receive more than 50 inches during the three winter months. Two stations in western North Carolina have winter averages of 21.8 inches; two stations in Mississippi have averages of 18 inches; three in Louisiana have averages of 16 inches; these latter averages mean that in many winters the totals are more than 20 inches.)

Some Consequences of Wet Seasons

The effects of wet seasons vary with their wetness, with the season of the year which is wet, and especially geographically. In arid regions, wet seasons are especially welcome, greatly increasing plant growth, and stock water supplies, raising reservoir levels, and stimulating hope that "the climate has changed for the better." In dry regions, however, transportation is often adversely affected by wet seasons, as bridges are few and usually small and most roads and railways are inadequately surfaced against much rain. Airports also are often rendered useless by wet weather, as normally in dry regions hard surfaced runways are still relatively few.

In the semiarid and subhumid regions, the effects of wet seasons, especially during the warmer months, are conspicuously significant. In such parts of our country, thousands of optimistic people are alert to benefit from the relatively abundant moisture which wet seasons supply to their rich soil. Hence there is a large expansion of cropped land, and increase of livestock. For example South Dakota and Kansas had about twice as many hogs in 1940, after the wet and hence good corn summer of 1939, as in 1937, after the drought year of 1936. In Kansas in the 25 years 1916–1940, the state average corn yield varied from 3 bushels per acre in 1934 and 4 bushels in 1936 to 30 bushels in 1927 and 27 bushels in 1928. The yield in wheat ranged from 8.5 bushels per acre in 1933 and 9.1 in 1935 to 18.5 bushels in 1931 and 16.3 in 1928 (Bean, '42). These great differences are of profound local economic importance.

The large crop yields of the wet seasons in regions generally rather dry often produce reckless extravagance, one significant form of which is in plowing up much additional sod.

In humid regions, wet seasons often mean poor harvests on the low land, and for some crops also upon land not flooded. For example, the damage to the wheat crop from rust, smut, chinch bugs and various other pests is greatly increased by wet weather. Most weeds grow relatively rapidly in wet weather, and cultivation is interfered with. A heavy crop of weed seed may take years to eradicate because some of the seeds do not germinate for years. The harvesting of crops, particularly of hay, is also badly interfered with by wet seasons.

Wet seasons are especially harmful upon lowlands which are flooded and upon cultivated hillsides, where soil erosion also is much increased.

In such a humid state as Indiana, wet seasons are not welcome except in summer. Wet summers usually are beneficial to the corn and oat crops, except on low ground. For example, the state average yield of corn was 51.5 bushels per acre in 1939, a wet summer, but was less than three-fourths as great (37 bushels) in 1940, a dry summer, and less than half as great (24.8 bushels per acre) in 1934, a very dry summer. Likewise Indiana's oat crop has varied from a state average of 45 bushels per acre in a favorable season to little more than a third as much (15.5 bushels) in the bad drought summer of 1934 (Visher, '44a).

The seasonal distribution of wet seasons is also of significance. Winters with exceptionally heavy precipitation imply heavy snowfall in the northern states, with many "snowbound" localities, and often with subsequent floods in late winter or spring. An exceptionally snowy winter, with its consequent partial filling of most undrained glacial depressions known as lake beds in eastern Dakota Territory in 1881, notably increased the rush of homesteading settlers in the next few years, producing "The Great Dakota Boom." These water bodies not only afforded domestic and stock water supplies but they gave a misleading suggestion of humidity. Much of what is now eastern South Dakota reported 100 inches of snowfall during the winter of 1880–81 (Visher, '18). The loss of livestock due to excessive snowfall is often serious in the range country. For example, more than half of the cattle of the region surrounding the Black Hills starved because grazing was prevented by heavy snow in 1886–1887, and no adequate supplies of feed were then available (Visher, '18).

The parts of the country which have seasonal totals of more than 15 inches of precipitation relatively frequently are the areas where the soil

is especially deficient in average fertility. This is largely a result of leaching of the more porous soils, and of erosion of sloping land. In the rainy Pacific Coast region, where more than 20 inches of rain commonly falls in winter and where the annual runoff is great, leaching has been serious, except on some glacial clay lands. In the Deep South, leaching has rendered most sandy soils almost sterile, while even on relatively gentle slopes soil erosion is rapid. Except for the low lying land along the Coast (where marshes or badly leached land prevail), fully four-fifths of the South has widespread "serious" or "harmful" erosion (Visher, '41a, b, '42).

When the long-time damage of leaching and soil erosion are considered, effects of encouraging farming in areas normally too dry for successful agriculture, it appears probable that the damage done in our country by exceptionally wet seasons outweighs the benefits which wet seasons yield in those parts of the country where they are welcome (Visher, '43).

Summary

Two maps for each of the four seasons reveal sharp contrasts in the amount of rainfall received in various parts of the United States in wet seasons. Two other maps for each season show the percentage of the seasons which receive large totals, 15 and 20 inches or more. In addition to affording concrete evidence of the widely recognized longitudinal contrasts, especially between the East, Rocky Mountains and Pacific Coast, these maps reveal frequent very heavy rainfalls in the Deep South. Wet seasons have various significant consequences, varying with the region, season and amount. The frequently very wet seasons in the South correlate with the extensive relatively infertile soils, with rapid soil erosion and with low average income and partly with race. It appears likely that wet seasons are even more harmful than exceptionally dry seasons, especially by increasing soil erosion and unwise land use, and, in the warmer areas, reducing human activity.

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ALGAE ON ANIMALS: A BIBLIOGRAPHICAL NOTE

Since seeing Louis G. Williams's paper on a green alga growing in tufts on small crabs on the coast of North Carolina, in Ecology for April, 1947 (pp. 204–207), and his colored slides of the same, shown at the Atlanta meeting of the Association of Southeastern Biologists, shortly before, I have found in literature, records of two comparable cases, one published long ago and one very recently.

In Garden and Forest (weekly, New York) for April 25, 1888, Prof. W. G. Farlow of Harvard University briefly summarized a report (not cited specifically) of Mme. A. Weber van Bosse on a green alga, *Trichosperma,* and a violet-colored one, *Cyanoderma,* growing in the hair of two genera of sloths, *Bradypus* and *Choloepus,* in European zoological gardens. The abstract does not indicate how many species there may be in these two genera of algae, and what their natural distribution may be, but

possibly some one who reads this may be able to get more details from Mme. van Bosse's paper or some other source.

Some of this information must have gotten into circulation through other channels, and at a much later date, for curiously enough one of "Uncle Ray's" syndicate articles (which deal mostly with natural history subjects), in daily papers of June 14, 1948 (about two months after I discovered Prof. Farlow's note), mentions that green algae sometimes grow in the fur of sloths (which are South American animals) in such abundance as to give the animal a green appearance. And although "Uncle Ray" did not say so, that undoubtedly serves as protective coloration, for the sloths are tree dwellers.

The latest instance is a note by R. M. Chute, on *Basicladia* in Maine, in RHODORA for September, 1949. *Basicladia* is a genus of algae, said to be found only on turtles, of several genera, more or less aquatic. Mr. Chute's note did not indicate the affinities of this genus, or the number of species in it; but following up some clues I was led to two papers by F. S. Collins, in RHODORA, 1907 and 1909, in one of which the first known species was described, under another generic name. And to one by William E. Hoffman and Josephine E. Tilden, in the BOTANICAL GAZETTE for June, 1930, in which the genus *Basicladia* (of the Cladophoraceae) was established. It was based on Collins's species, from Michigan (later found by him in Massachusetts), and a new one from Minnesota.

These 1909 and 1930 papers both refer to another genus of green algae, *Dermatophyton*, that had been found on turtles in Europe, as long ago as 1887. Collins, in his second paper, said it had been found once in this country, but without indicating where, when or by whom. Apparently these algae on turtles are rather rare, or have been overlooked by persons who were studying turtles and not algae; but where they do occur they must be of some service for protective coloration; a case of symbiosis, like those on the sloths. It would be interesting to speculate on how these algae have been evolved and distributed, but there does not seem to be much prospect of ever getting the whole story.

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A NORTHERN CLIMAX, FOREST OR MUSKEG?

Without becoming involved in pure concepts of climatic climaxes, the observant traveler in Southeast Alaska may be impressed with the extent and apparent aggressiveness of muskeg areas. This in a region described as consisting of "fiords and forests."

In traveling by air one notices vast areas, often much of entire islands (Dachnowski-Stokes, '41: figs. 4 and 5) in Southeast Alaska, are covered by long sweeps of yellow and brown muskeg broken by patches and fringes of scrubby timber, shrub areas, ponds, rocky elevations and drainage channels. The drainage channels are usually bordered by a narrow fringe of tree growth which may consist of any of the native tree species. They are almost invariably of poor form and vigor.

In general, from sea level, the extent of muskeg types in the region is not apparent. When traveling by water, the observer sees the vertical aspects of the land masses which give the illusion of endless forests from shoreline to timberline. Local topography plays an important part in Southeast Alaska's local weather and vegetation. Figure 1 presents a schematic sketch of a very common land form not apparent from the water level.

To the foot traveler, the phenomena of this region unfold to show such surprising items as muskegs on slopes, ponds on slopes maintaining themselves by growing their own dams, and pot holes or ponds on the very crests of ridges and hummocks or on the very brink of abrupt slopes of drainages. Figure 2 is a photograph of a common typical muskeg type in Southeastern Alaska. The terrain is sloping, pothole ponds occur at several different levels, stunted lodgepole pine (*Pinus contorta* Dougl.) is the principal tree species, and a better class of timber occurs on the steeper slope in the background.

To the writer's knowledge, little consideration has been given to the place of muskeg in the successional series in this region. After several seasons of timber cruising at several widely separated localities in the region, it appears to the writer that muskeg represents a physiographic climax over much of this region. Furthermore, this physiographic climax may be increasing at the expense of what is usually accepted as climatic climax vegetation, *viz.* forest cover, by a slow but progressive process of site deterioration within certain topographic limits.

This conclusion is based on the observation of the following phenomena:

1. The over-abundant and well-distributed rainfall providing a general surplus of moisture tending to inhibit decay of organic matter. Mean yearly precipitation at Juneau, Sitka and Ketchikan is 84, 87 and 159 inches, respectively. At higher elevations it is probably greater.

2. Cool temperatures and paucity of sunshine

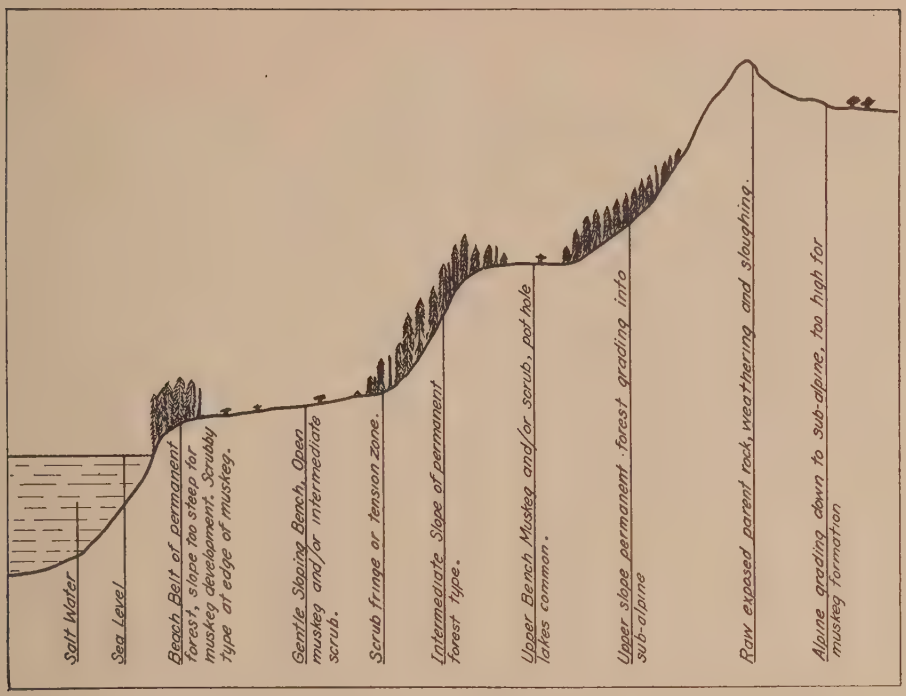
Salt Water
Sea Level
Beach Belt of permanent forest, slope too steep for muskeg development. Scrubby type at edge of muskeg.
Gentle Sloping Bench. Open muskeg and/or intermediate scrub.
Scrub fringe or tension zone.
Intermediate Slope of permanent forest type.
Upper Bench Muskeg and/or scrub, pot hole lakes common.
Upper slope permanent forest grading into sub-alpine
Raw exposed parent rock, weathering and sloughing.
Alpine grading down to sub-alpine, too high for muskeg formation

FIG. 1. Schematic profile diagram of the relationship of forest to muskeg in Southeastern Alaska, between sea level and timberline.

FIG. 2. A typical muskeg type common on the more level areas of Southeastern Alaska. The small deformed trees are lodgepole pines. Pothole ponds are to be seen at left and right in the foreground, and snow patches in the background at the right. Photo No. 194090 by U. S. Forest Service.

also hinder decay, evaporation and transpiration. The mean summer temperature is between 50° and 55°. Conversely, the mild climate favors vegetative growth.

3. The tendency which accumulating organic matter has to waterlog areas unless slopes are steep enough for gravity to maintain drainage.

4. The apparent deterioration of the forest bordering muskegs. Snags, unthrifty trees and poorly competitive species like lodgepole pine and mountain hemlock (*Tsuga mertensiana* (Bong.) Sarg.) characteristically border the muskeg or make up extensive areas of poorly drained sites. Scrub and muskeg areas are commonly of gentle to moderate slope which appears inadequate to promote enough drainage to maintain a good forest growing site.

5. The fact that substratum does not inhibit muskeg formation. Profiles reported by Dachnowski-Stokes ('41: figs. 3, 6, 8) occur on a variety of formations.

Discussion

The crux of the situation centers around the impact of excessive moisture in a region of a relatively cold climate mild enough to produce luxuriant vegetation. Organic material with its affinity for moisture impedes drainage and aggravates the necessity of adequate drainage for vigorous tree growth.

Forest types as such in Southeast Alaska are rather complex communities. Present logging operations are in subclimax stands which are often the pioneer or invasion forest types usually having a large proportion of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) following glacier recession, river valley filling, land slides, windthrow, fire, and old cuttings. In short, merchantable sawtimber stands under present conditions are usually maturing spruce stands of even-age character, whereas the older, commercially less valuable over-mature climax stands have progressed to an all-aged community of largely defective, suppressed, slow-growing hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and cedar (*Thuja plicata* Donn., and *Chamaecyparis nootkatensis* (Lamb.) Spach.) on more mature soils. If a muskeg climax theory is correct, these accepted climax forests are just a later stage than the thrifty subclimax types in the progressive succession to muskeg within the *altitudinal* and *gradient* limits for peat formation.

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BOOK REVIEWS

Review and Critique of Recent Work on Biogeography by Jeannel[1]

To the biological systematist who looks beyond the task of analyzing and comparing the morphological differences which his work brings to light, one of the most interesting fields of thought, and often of speculation, is that concerning the factors which underlie the distribution of the subjects of his investigations.

The broad generalizations on biogeography which have been given us usually have come from the pens of men who were not special students of any particular class of animals or plants, but from thinkers of a philosophical turn of mind, their detailed evidence pro or con drawn chiefly from the work of special students in this or that field. But infrequently in zoology and botany has the special student utilized the geographic evidence supplied by his meticulous morphological studies in his field of work, and given to us his own interpretation of biogeography on a global basis.

During the war years, however, such a work appeared from the pen of a distinguished French entomologist, Dr. René Jeannel, of the French National Museum of Natural History, and owing to the infrequency of such treatises it is particularly welcome. This interesting and arresting study is entitled, "La Genèse des Faunes Terrestres: Éléments de Biogéographie." Owing to the fact that publications issued during the war years, particularly in continental Europe, may escape the attention of students elsewhere, it is important that Dr. Jeannel's most absorbing and provocative work should be known to those particularly interested in broad biogeographic problems.

The preface opens with the comment that "this work is chiefly the statement of biogeographic facts assembled in the course of thirty-five years of systematic research on certain groups of insects." The author promptly disclaims the pretension of writing a treatise on biogeography, but adds that instead he wishes to set forth much new and diverse material "drawn from a very great variety of living things." He adds, however, that he has relied chiefly upon his "works on the Coleoptera, to reassemble solid elements of an essay on the genesis of terrestrial faunas." In consequence in the pages of this very important study there is summarized a vast amount of distributional information drawn mainly from Dr. Jeannel's numerous studies, and there is also presented a number of generalizations from this evidence. However, in many cases these conclusions are presented with little or no supporting or correlated evidence drawn from other groups of animals, or even other orders of insects.

In his preface Dr. Jeannel states very bluntly that for reasons which are there set forth, the work is "very personal." He also says, with a finality which some other biologists could also use, that "tout d'abord, je suis lamarckien." He adds that all his researches on cavernicolous animals have convinced him more and more of the reality of the old principle of Lamarck. To those who may doubt the weight behind this conviction it should be said that Dr. Jeannel is probably the world's leading authority on cavernicolous Coleoptera, that in this latter assemblage is a vast array of genera and species found in no other situations, and also that morphological modifications in these insects are of the most remarkable and unusual types; hence adaptation has clearly played a very great part in their evolution.

With a frankness equal to that proclaiming his Lamarckian faith, Dr. Jeannel also states he "is Wegenerian," and through the many pages of his "Genèse" he has presented and discussed his voluminous evidence from the point of view of continental drift, and he has probably presented the greatest amount of information drawn from a limited field of work which has been advanced so far in support of the Wegener theory. Unfortunately at times it seems the "wish is father to the thought," and that Dr. Jeannel's reasoning is labored, quite circuitous and hardly convincing. In my own experience I have found the attitude of open-minded students of biogeography toward continental drift is that, as far as present evidence goes, it merits the Scotch verdict of "case not proven." Also from a number of Dr. Jeannel's drift illustrations a radically different interpretation is possible.

Dr. Jeannel's work suffers from two main weaknesses, the more conspicuous of which is that though he has summarized most of the theories relating to biogeography, he has completely failed to consider, or even mention, the work of outstanding scholars who have made most important and epochal contributions to the subject, as for instance the late Dr. W. D. Mathew's "Climate and Evolution" (1915), which remains a classic whether one agrees or disagrees with his conclusions. In other cases no consideration has been given to the great and final work of such masters as Schuchert published subsequent to 1929, yet those of authors who have supported drift published long after that time are listed in the bibliography. Many

[1] **Jeannel, René.** 1942. La genèse des faunes terrestres: Éléments de biogéographie. Paris: Presses Universitaires de France. Pp. viii + 511, 8 pls.

important contributions made to the subject by American and other systematic biologists of broad experience with biogeography have, in their implications, been almost entirely ignored, even where their more intimate or special field of work is concerned. Among these names may be mentioned Barbour, Pilsbry, Merrill, Gleason, James Chapin, Bequaert, C. C. Adams, Montague Cooke, Maynard Metcalf, Launcelot Harrison, Stresemann, Lönnberg, Ernst Mayr, and numerous others. In a few cases the original conclusions of these men are quoted second-hand from a subsequent reviewer or encyclopedist, rather than from the original, and no credit is there given to the actual author of the statement.

I have no intention or desire to debate continental drift with Dr. Jeannel or any one else, because I am not a geologist, and the geologists themselves are very deeply and sharply divided on the validity of the theory. They and the geophysicists should eventually be able to tell us whether the continents have or have not drifted, and whether the oceanic basins have been permanent or merely sliding boards for wandering slabs of rock. Some of us do believe in land bridges, however, not to the Scharffian extent, but most certainly in some. Even the "drift" proponents are forced to fall back on land bridges at times, after their continents have wandered to their present positions, and further distribution remains to be explained.

With some of Dr. Jeannel's conclusions regarding the factors controlling the distribution of life in Africa, I disagree basically, and in this I find I have the support of other American students of African zoology, who have had many years of field experience in that continent. The basic difference I would state here is that temperature, which is given the leading position by Dr. Jeannel, is, in the opinion of the other school of thought, secondary to humidity, which in Africa, as well as in tropical America, is the major factor controlling the distribution of life.

I do, however, wish to take issue with some of Dr. Jeannel's general conclusions as to the movements of certain elements of the North American fauna, the latter a subject with which I have been most intimately associated, in both the field and the laboratory, for nearly half a century, working in certain orders of insects and also in several fields of vertebrates. I have also enjoyed years of association with many scholars working intimately in the field, as well as in the laboratory, with other elements of our North and South American fauna and flora. In consequence the comments here presented are drawn from a relatively broad field, and not solely from the circumscribed one of my own specialty.

No thoughtful student of the North American biota can decline to recognize the essential unity of the elements to which the term Holarctic has been applied. Their common origin becomes increasingly apparent the more critically one studies the subject. Similarly convincing is the evidence as to the location of the area which made this continuity so much of a reality. However, in discussing the movement of lines of Angaran origin into North America, Dr. Jeannel makes the following axiomatic declaration: "for their distribution in the New World, these lines have utilized chiefly the North Atlantic lands." After brushing aside the conclusions of numerous biogeographers that the great bulk of the Angaran immigrants into North America reached it by way of a connection between northwestern North America and eastern Asia, he dismisses this postulate by stating that "the successive positions of the North Pole in the course of the Secondary and Tertiary renders very improbable a great exchange of fauna and flora by this route." As I understand it polar shift is still a debatable theory, while the evidence for a Bering Sea connection between the continents rests on a relative mountain of evidence—hydrographic, zoological and botanical. On the contrary conclusive evidence of the passage of forms of life across the present north polar area to North America is still lacking, along with concrete evidence that terra firma has existed in these high latitudes in relatively recent geological times.

The biotic evidence for an inter-continental connection of North America and eastern Asia in at least certain periods of the past is exceedingly extensive, and even a summarized presentation of it would fill many pages, but a limited number of representative illustrations, drawn from numerous groups, will serve to illustrate the point. These are here grouped under major classificatory headings.

Mammals. The chipmunks of the genus *Eutamias* are found only in the western portion of North America and in northern China west to Sze-chuan, being absent from Europe, while in eastern North America they are replaced by the allied genus *Tamias*. The spermophiles of the restricted genus *Citellus* are of broad distribution in Eurasia west to Russia and in the western and central parts of North America, but are absent from western Europe and the eastern portion of North America. The flying squirrels are broadly distributed in North America, in Malaysia, and in eastern and central Asia, and west to Scandinavia and central Europe but are absent from western Europe. The voles of the genus *Lagurus* do not occur in eastern North America east of North Dakota, while in Eurasia they extend from Mongolia to southern Russia. The family Ochotonidae,

or pikas, occur in North America only in alpine habitats in the western mountains, being completely absent from all the eastern mountains or other boreal areas in the same region, while in the Old World they are distributed from southeastern Europe to northern and central Asia. The family Zapodidae, or jumping mice, are broadly distributed over North America, and one subgenus (*Eozapus*), with a single species, occurs in Sze-chuan, China. The brown bears of western North America are more closely related to the Old World bears of the restricted subgenus *Ursus* than they are to *Euarctos,* which is the more broadly ranging North American subgenus, and the only one represented in eastern North America. The American badger (*Taxidea*) is entirely absent from eastern North America, but broadly distributed in the west, while various other genera of the group occur in the Old World, *Meles* broadly so in Europe. The small wolves of the subgenus *Thos* are broadly distributed in Asia and Africa, but in North America (as the coyotes) are found only in the west and central portions, being completely absent from all of the East. The shrews of the subfamily Uropsilinae comprise the genus *Urotrichus* from the mountains of Japan, *Uropsilus* from Central Asia, and *Neurotrichus* from coastal northwestern North America. The much closer relationship of the forms of the North American wapiti (*Cervus canadensis*) to the Central Asian members of the genus *Cervus* than to the red deer (*C. elaphas*) of Europe is well known. The distribution and complexity of the caribous, or reindeer, of the genus *Rangifer* would indicate that the genus passed through a marked period of its development in western North America, where two distinct lines of the genus and a number of forms are found, while but one of these lines (the true reindeer) is found in the Old World and has not survived in western Europe in historic times, although it was, and is, better adapted to Ice Age conditions than any other deer. The wild sheep of the genus *Ovis* are found in north central and northeastern Asia and in suitable areas of western North America, but have always been absent from eastern North America and Europe. The genus *Oreamnos* (the "mountain goat") of the mountains of northwestern North America has its nearest relative in the Malayan and eastern and central Asian genus *Nemorhoedus,* and has no near relatives in Europe or the eastern portion of North America. We need only to mention the Tertiary history of the camels to give clearly an important stock which travelled eastward into Asia from America, and not by North Atlantic lands.

Birds. In North America the magpies (*Pica*) are restricted to the western portion, and the dominant form is but a subspecies of the Eurasian one. The rosy finches of the genus *Leucosticte* occur only in the colder parts of eastern and central Asia and western North America. The "varied thrush" (*Ixoreus*) of northwestern North America is most nearly related to *Cichloselys* of northeastern Asia. The bluebirds of North America (*Sialia*) also are most nearly related to the Himalayan genus *Grandala.*

Reptiles. Material of the side-striped lizard (*Liolepisma laterale*) from the eastern United States and from Japan has been considered inseparable by Stejneger; other species of the genus are all Old World. In the United States the species is broadly distributed in the Lower Austral Life Zone. The lizards of the genus *Eumeces,* while absent from Europe, most of Asia and the greater portion of Africa, are found in North and Central America, eastern and southwestern Asia and North Africa.

Amphibians. The bell toads of the Discoglossidae, which have a broad but disconnected distribution in the Old World, clearly reached extreme western North America from eastern Asia, and are entirely absent from all the remainder of North America.

Mollusks. The zonitoid genus *Pristoloma* has fourteen species, representing two subgenera, occurring in the Pacific coastal region of North America from Alaska to California and inland to Montana and Utah, while a single species (*P. japonicum*), of the north island of Japan, is the only species found beyond the limits of North America. In his recent monumental work on North American land mollusks Dr. H. A. Pilsbry, who is our greatest living authority on that subject, has stated, "So far as the evidence goes, it appears that the ancestors of the large land snails of West America began to come in from Asia during Cretaceous times." In the same work he has shown that the limacid genus *Deroceras* very probably invaded America from Asia in the middle or late Tertiary, spreading southward through the western states, and he adds that like many other western (i.e. in North America) snails of palearctic origin it is "not known to have penetrated into the eastern part of the continent." He further shows that while the family Arionidae is Holarctic, in North America it is found as an endemic solely in the western part. The family Helicinidae, as Pilsbry has shown, inhabits tropical and north temperate America, the eastern border of Asia from Japan south, and also occurs in many islands of the Pacific.

Insects: Orthoptera. The cockroaches of the family Panesthiidae with a single exception are limited in distribution to eastern and southeastern Asia, Indo-Malaysia, Australia and Melanesia. The one exception is the genus *Cryptocercus,* the genotype of which is North American, with two widely separated areas of distribution, one in the eastern Appalachians

and the other in the Cascade-Sierra Nevada chain, some thousands of miles apart. In recent years the genus *Cryptocercus* has been discovered in eastern Asia. A virtual parallel to *Cryptocercus* is the locust genus *Zubovskya,* which has a similar type of discontinuous distribution in North America, except that the eastern area is more extensive and the western one even more limited, while several species are known from the mainland of eastern Asia. The locust genus *Podisma* is a dominant Eurasian genus, yet a single species (*P. hesperus*) is found in the Cascades of Oregon, the relationship of which is nearest to a species of the northern island of Japan. The North American locust genera *Appalachia* and *Dendrotettix* are more nearly related to *Podisma* and the eastern Asiatic *Ognevia* and *Eirenephilus* than to any other genera. Of these two North American genera the first is restricted to eastern areas, while the second is found in the same region west to Oklahoma and Texas, and has the unusual locust habit of attacking and defoliating woodland trees in locally circumscribed but very devastating outbreaks, and we now know that the related *Eirenephilus* has similar habits in Japan.

The locust genus *Melanoplus* is probably the most diversely developed and specifically complex genus of true locusts, having in excess of one hundred and fifty valid species known from North America south to the Mexican Tableland. It is clearly one which has long been North American in its distribution, and it is the most widely distributed and adaptive of any locust genus found in that continent. A single species (*M. frigidus*) found in Alaska has penetrated Eurasia, and reached westward as far as Scandinavia and the Alps. Among the more than two score of New World genera of the tribe Podismini (Melanopli of Scudder), to which *Melanoplus* belongs, and which range from Alaska to Argentina, represented by more than three hundred species, aside from those already mentioned but four North American genera (*Bradynotes, Asemoplus, Prumnacris* and *Buckellacris*) show at all close relationship to Angaran ones. The Podismini has been assumed by most European workers to be of Eurasian origin, but the enormous diversity of the New World representation seriously suggests that it may be an intrusive in Eurasia from America, and the nearest affinities of the above mentioned North American genera with Eurasian ones are clearly with certain of these from eastern and central Asia, and not with European types.

The very distinctive oedipodid locust genus *Aerochoreutes* is an inhabitant of the northern Great Plains and the northern portion of the Great Basin of North America. It is a steppe form and its nearest relative is the Eurasian *Bryodema,* which occur over a large part of northern Asia and eastern Europe. Clearly our *Aerochoreutes* is of Angaran derivation, and it is equally clear that its ancestral stock reached North America by a Bering Sea route in a period of relative aridity and restricted forest areas. The katydid subfamily Decticinae is highly developed in the northern hemisphere, with, however, certain genera found in South Africa. From eastern North America but two genera have been referred to it, while in the western section there is found a considerable number of genera, which possess in common with many from the Old World highly specialized patterns of life. One of the eastern genera is the flightless *Atlanticus,* of which seven species are known from the country to the east of the Great Plains. No species of the genus occurs in North America west of that line, but in the last few decades a number of species of *Atlanticus* have been discovered in eastern Asia, in territory reaching as far north as the Ussuri district of Siberia. In the eastern United States at least two species of the genus have reoccupied land which was solidly glaciated by at least three distinct ice sheets.

One of the strangest of all known Orthoptera is the genus *Grylloblatta,* and the exact position of the family containing it has long been debated. It was first described from the northern Rocky Mountains (*G. campodeiformis*), and other species are now known from the Cascades and Sierra Nevada ranges, while two species, subgenerically distinct, have been discovered in Japan. No other members of this undoubtedly primitive and probably senescent family are known. Individuals of some of the species live under a condition of atmospheric saturation but slightly above freezing, along the margins of glaciers or ice pockets, and although suitable conditions exist in many areas of northern Asia aside from the extreme eastern border, this very remarkable insect has not been encountered elsewhere. It is possible this living fossil is an ancient Laurentian type, and that in the Pleistocene it was more widely spread along the front of the great continental glaciers, and that today it survives only in a few places where conditions remain favorable.

Plants. The evidence supplied by the plants leaves little doubt as to the connection of North America and Eurasia having been by a Siberian-Alaskan land-bridge. The well-known fact that scores of existing genera of trees and other plants are today common to eastern North America and eastern Asia has been cited by many authors. Most of these genera are unknown as existing forms in Europe, and for at least certain of them we have no paleontological evidence of their former occurrence there. Among outstanding trees may be mentioned the magnolias (*Magnolia*), the witch hazels (*Hama-*

melis), the tulip tree (*Liriodendron*), the honey locusts (*Gleditschia*), the Kentucky coffee tree (*Gymnocladus*), the gum trees (*Nyssa*), the sassafras (*Sassafras*), and the various forms of spice bush (*Benzoin*). This biota was clearly an older one than that represented by genera found only in the western portion of North America and in eastern Asia. The latter complex also is more typically represented in the Cascade-Sierra Nevada and Pacific coast ranges than in the Rocky Mountains.

Dr. Jeannel has expressed his belief that it is in the Rocky Mountains one finds the greatest amount of evidence of Angaran intrusives in North America. While this is true for a number of groups, there is more evidence of Asiatic relationship to be found in the biota of the Cascade-Sierra Nevada and Coast Range mountains in the United States, and the immediate Pacific belt to the north. In these areas will be found the more recently arrived, less modified Asiatic types, some of which doubtless owe their present areal distribution to the milder interglacial periods, which in parts of the United States were almost tropical in their faunal characteristics, with their abundant remains of tapirs, ground sloths, great cats, and non-Arctic elephants and mastodons, as for instance in the deposits at Big Bone Lick, Rancho La Brea, and Port Kennedy. There is probably no part of the world regarding which our knowledge of Tertiary, and particularly Pleistocene, conditions has been augmented on a greater scale in recent years than North America, and the relevant literature of the past few decades is voluminous and illuminating. Unfortunately this literature seems to be much less known abroad than is warranted by its importance in the interpretation of the factors underlying the present distribution of life in the New World.

Dr. Jeannel has referred in his work to the function of the meridian mountain chain of the New World in supplying a means for continuous north and south distribution of life in that hemisphere. Unfortunately this theory is unsupported by orographic evidence, and has long been consigned by American students to the limbo of unsound elementary geography. While the Andes do supply a consistently high mountain area from the Straits of Magellan to Colombia, the same is not true of the great areas to the north. In Central America there are a number of marked breaks, and the old Central American mountain mass has a far more general east and west disposition of its numerous ranges, with often relatively low intervening valleys, which probably have always contained a different biota from the higher levels. The Isthmus of Tehuantepec is very definitely a low area, and a very decided break in any supposed mountain continuity, and its known geologic role as an oceanic portal is further evidence of this deplanation. The Panama portal has also been discussed at length by American paleogeographers and biogeographers. The special character and distinctive biotic role of the Mexican Tableland is not that of a continuous mountain pathway for traffic bound in either direction, and within the southwestern United States there is no continuity of a high meridian mountain range until one reaches northern New Mexico or the great Arizona Plateau. The many mountain ranges of southern California, Arizona and New Mexico and western Texas are not parts of continuous chains, but are detached individual ranges or systems, surrounded by plains or steppes, which are usually of Sonoran desert character. It is not until one travels as far northward as Wyoming that a continuous meridian mountain system extending far to the north is again encountered. Further the Basin and Range Province (the so-called "Great Basin") of the United States, which lies between the Rocky Mountains and the Sierran system, and which is sometimes roughly included in the concept of the former, has had a biotic individuality in the recent past which is increasingly emphasized in our steadily augmenting knowledge of its Pleistocene history.

Dr. Jeannel deserves our thanks for his presentation of a great mass of documentation, which cannot fail to be of the greatest service to other and future workers in biogeography. While their interpretation of the movements of the forms which he discusses may not fully agree with his conclusions on the same, most certainly he has presented his views broadly and vigorously. Whether one believes in continental drift or does not do so, "La Genèse" is of lasting importance in the study of biogeography. Also by his broad statement that the role of adaptation in the Lamarckian sense is strongly supported by his years of study of a group of insects possessing a very high degree of adaptation to cavernicolous life, Dr. Jeannel has earned the thanks of those who from similar systematic studies of other insects, as well as from the evidence of paleontology, feel that environmental factors can and must leave their mark on an organism.

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McDougall's Plant Ecology, "Thoroughly Revised" [1]

A new edition of a standard plant ecology text is rightfully hailed as a landmark in the development of a science, especially when it is conspicuously designated as "thoroughly revised." Consequently we open the book with much anticipation and page through it. Something more than a familiar appearance strikes our eye. This is not our friend of eight years ago rejuvenated and dressed in modern style. Rather, it takes an extra effort to find a new feather tucked here and there into the bonnet of a decade ago.

It seemed desirable to obtain a reasonably precise knowledge of the changes appearing in this edition, contrasting it with the third edition of 1941 (itself not too different from the first edition of 1927). With this in mind, the two editions were "proofread" against each other paragraph by paragraph. First, last, and several intermediate sentences of each paragraph were checked against each other; but other sentences were not compared and consequently certain revisions may have been overlooked.

In this comparison, the following data were obtained: The entire book is completely reset, with more words per line, resulting in a decrease in number of pages from 285 to 234. The twenty-two chapter headings are identical. The 156 numbered section headings of the third edition are repeated without change, except for the rewording of one title, and the addition of two new sections, new nos. 135 and 156. The frontispiece is new. The old frontispiece replaces old figure 81. The entire 118 figures are otherwise identical, except that figures 46 and 78 have been replaced by two new photos on the same subjects. Almost all the figures of the copy of the third edition available to me showed excellent contrast of dark and light, whereas those of the fourth edition were distinctly gray in comparison. Literature references at the end of each chapter always have at least one change, with the elimination of older references and the insertion of newer ones. The appendix remains unaltered. The paragraph by paragraph comparison of the entire volume revealed a grand total of 34 differences, in almost every case being changes in not more than a few lines, sometimes in only a few words. Nineteen can be classed as amplifications or the insertions of additional examples. One is the rewording of what had been an ambiguity. One, the very first paragraph of the book, is a rephrasing for greater literary value. One is a replacement of a paragraph by one on a different subject. Four are the corrections of what had been minor errors. Eight concern changes related to recent scientific advances. Of these eight, seven represent a minimum of rewording so that the remainder of the paragraph is no longer incorrect. For example, "Ten chemical elements are necessary as food materials" becomes "At least ten . . ."; and "Maximov . . . believes that solar radiation and an actual shortage of water . . . induce xeromorphic structures" becomes "It is believed that solar radiation . . ." The eighth of these is the one and only significant improvement in the fourth edition, the insertion of new section no. 135, "Past Successions Determined by Pollen Analysis," occupying most of page 179. These differences are mentioned for the benefit of those who may still wish to use the third edition.

The above analysis makes one wonder whether the use of the word "edition" is not undergoing a change in our language. If not, then one is led to query at least the propriety of this action on the part of both author and publisher. All the changes made are ones which could have been handled by a professor during the course of his teaching, with no discredit to the book or its author considering its 1941 date. In print, however, the effect is to nullify the cash value of second-hand third editions for money-short students, to change all page references in one's teaching schedule, and to complicate the situation for all future librarians and bibliographers. It will be interesting to see whether the third edition continues to be demanded for some courses.

The significance of the changes in this edition has still further import, and that is in the progress of the field of knowledge since the third edition of 1941 and the first edition of 1927. The author tries to clarify this point in his statement in the preface, "Although many excellent papers and some books on ecological subjects have been published during recent years, most of them have not changed our fundamental thinking to any great extent." Regretfully, the reader is left in doubt as to whether this refers to the author himself, or to the science as others know it.

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[1] **McDougall, W. B.** 1949. Plant ecology. Fourth edition, thoroughly revised. Philadelphia: Lea & Febiger. Pp. 234. $4.00.